GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS BEARING
ON HEREDITY AND VARIATION

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GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS BEARING ON HEREDITY AND VARIATION

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CORRIGENDA

Page 49, first formula, for numerator, instead of "$\Sigma(yE)/N=\bar{y}\bar{E}$," read "$\Sigma(yE)/N-\bar{y}\bar{E}$".

Page 50, first formula, for "$E=(\bar{E}-r\frac{\sigma_E}{\sigma_y})\bar{y}+r\frac{\sigma_E}{\sigma_y}y$" read "$E=(\bar{E}-r\frac{\sigma_E}{\sigma_y}\bar{y})+r\frac{\sigma_E}{\sigma_y}y$".

Page 69, fourth formula from bottom, numerator, for "$r_{ye_1}-r_{ye_2}r_{e_{12}e_1}$" read "$r_{ye_1}-r_{ye_{12}}r_{e_{12}e_1}$".

Page 99, fifth line of footnote, for "SEWELL WRIGHT", read "SEWALL WRIGHT".

Page 99, last line of footnote, for "B_n F_{n-1} G_{n-1}" read "B_n—F_{n-1}—G_{n-1}".

Page 117, interchange lines 18 and 19, placing "in sections (12), (13) and (14)" above the preceding line.

Page 144, fourth line from bottom, for "$2p(p+q+t)+qs+pt$" read "$2q(p+q+t)+qs+pt$".

Page 146, last line, for "$(r+1)(p+q)(p+q+s+t)$" read "$(r+1)(p+q)(p+q+2s+2t)$".

Page 154, near middle, first expression in "Column 1" of table, for "$\frac{2^{n-1}+1}{2^{n-1}}+v^n$" read "$\frac{2^{n-1}-1}{2^{n-1}}+v^n$".

Page 217, legend of fig. 3, for "*pycuella*" read "*pycnella*".

Page 267, table 1, last line of third section, Ear No., for "(96-6)-4-1-6-8" read "(69-6)-4-1-6-8".

Page 268, line 13, for "±0.143" read "±0.119".
line 28, for "38 few seeds striped"' read "28 few seeds striped".
line 29, for "254" read "244" and ratio per 4, for "3.107 : 0.893" read "3.079 : 0.921".
line 30, for "0.107" read "0.079".
line 31, for "±0.065" read "±0.075".

Page 270, table 2, first line below heading, for "| 21 | 71 | 8" read "| 19 | 72 | 9".

Page 270, table 2, third line from bottom, for "| — | 79 | 21" read "| 3 | 76 | 21".

Page 274, line 6, for "324" read "824".
line 25, for "445" read "446".
line 28, for "40.4" read "42.4".
last line, for "1.229 : 2.771" read "1.225 : 2.775".

Page 279, line 24, for "36" read "30".
line 25, for "58" read "64", and for "2" read "3".
line 26, for "4" read "2".

Page 329, for lines 11-14 substitute the following:
"quence (rel. freq.) of the mating. For example 3 out of 50 fathers are very tall; if such married very tall women proportionally, then 3 out of 50 choices of such women should be made by very tall men; actually $8.4 = 3 \times 2.8$ is the proportion; whence 2.8 is the preference factor".

Page 330, table A, second column, totals, for "137" read "50"; fifth column, first entry, for "2.9" read "2.8", and fifth entry, for "1.0" read "0.1".

Page 379, line 16, for "nals, all males, and about 132 cm tall" read "mother, approximately 106 cm tall".

Pages 388, 389. The following citations should have been included:

CUSHING, H., 1911 Dyspituitarism. Harvey Lectures 1910-'11. pp. 31-45. New York: Lippincott.

DALE, H. H., 1915 The physiology of the thyroid gland. The Practitioner **94**: 16-25.

DOCK, G., 1915 The pituitary body and other glands of internal secretion. Modern Medicine, ed. by W. Osler and T. McCrae. **4**: 804.

PLATE, L., 1913 Vererbungslehre mit besonderer Berücksichtigung des Menschen, für Studierende, Ärzte und Züchter. pp. xii + 519. Leipzig: Wilhelm Engelmann.

PREUSS, J. D. E., 1832-1834 Friedrich der Grosse. Eine Lebensgeschichte. 5 vols. Berlin: Nauck.

WEINBERG, W., 1912 Zur Vererbung des Zwergwuchses. Arch. f. Rass.- u. Gesell.- Biol. **9**: 710-717.

Page 394, line 17, for "are" read "is".

Page 397, fifth formula under F_2 in class 1, for "*ggHh*" read "*ggHH*".

Page 398, line 18, for "4, 5 and 6" read "4 and 5".

Page 416, omit line 27, "1917 Genetical studies etc."

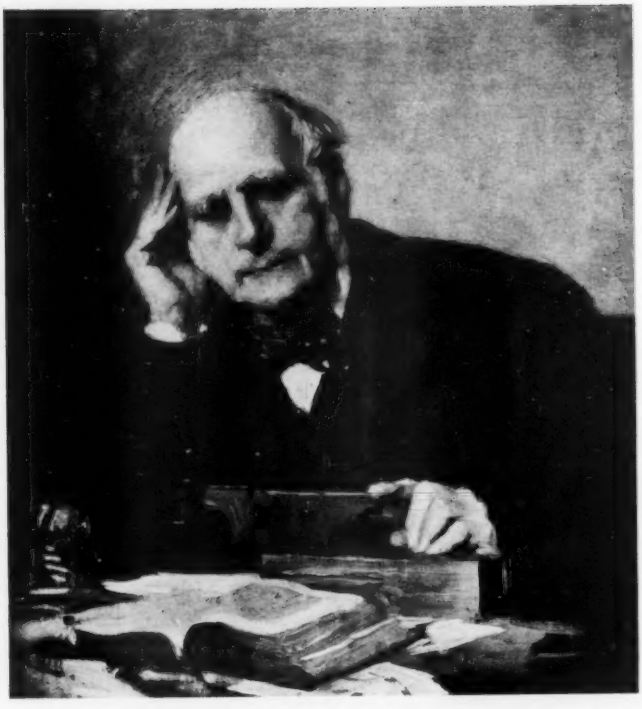
Page 439, middle of page, section heading, for "MATIGS" read "MATINGS".

Page 469, line 29, for "types" read "type".

Page 472, line 27, for "6 factors" read "9 factors".

Page 475, table 3, heading for "chromsomes" read "chromosome".

Page 504, line 6, for "Limit" $n =$ read "Limit" $n = \infty$.



Yours affectionately
Francis Galton

FRONTISPIECE—SIR FRANCIS GALTON

FRANCIS GALTON was born at "The Larches" in Sparksbrook, Birmingham, England, February 16, 1822, and died January 17, 1911. A precocious child, grandson of ERASMUS DARWIN by his second wife, and thus a half first cousin of Sir CHARLES DARWIN, heir to a fortune adequate to support him comfortably without dependence upon his own earning capacity, and handicapped by frequent and serious illness, GALTON strikingly illustrated by his own career the truth of his view that mental qualities are mostly innate and little affected by education and environment. He made distinguished contributions in several fields of science,—geography, meterology, anthropometry, experimental psychology, statistical theory, and genetics. Although he began his work in biological fields relatively late in life, his achievements have been truly epoch-making. His initial paper in this field was "Hereditary talent and character," published in *Macmillans Magazine* in 1865. His more important publications in the field of anthropometry, statistical theory, variation and heredity were "Hereditary genius" (1869), "English men of science, their nature and nurture" (1874), "Human faculty" (1883), "Life history album" (1884), "Record of family faculties" (1884), "Natural inheritance" (1889), "Finger prints" (1893), "Finger print directory" (1895), "Noteworthy families" (1906). He also published more than one hundred memoirs dealing with his investigations in blood transfusion in rabbits, heredity in man (stature, eye color, temper), heredity in sweet peas, in moths, and in Basset hounds; with anthropometry and the development of statistical theory and method and their application to problems of heredity and eugenics.

His influence on science in general and on genetics in particular can not, however, be measured by the extent of his own writings merely. FRANCIS GALTON was throughout his long life an able and active executive. His family, his financial independence, and his scientific position gained by early and important African exploration, gave him free contact with the influential men of his day, and his gentle but powerful influence was potent in many important movements. To instance only activities related to anthropometry and genetics, he founded an anthropometric laboratory in 1882, the BIOMETRIC LABORATORY in 1894 (so-named in 1900 when the journal "*Biometrika*" was established), originated the eugenics movement in 1901, establishing in 1904 an "EUGENICS OFFICE" which was later (1907) transformed into the EUGENICS LABORATORY in association with the BIOMETRIC LABORATORY at UNIVERSITY COLLEGE, London. At his death he bequeathed his residuary estate, amounting to about £45000, to the UNIVERSITY OF LONDON to found

the GALTON PROFESSORSHIP OF EUGENICS and to endow the FRANCIS GALTON LABORATORY FOR NATIONAL EUGENICS.

Unlike the work of MENDEL, GALTON's work received the highest contemporary recognition and he received many honors, among which may be mentioned six medals from the ROYAL GEOGRAPHICAL SOCIETY, the ROYAL SOCIETY, the ANTHROPOLOGICAL INSTITUTE, and the LINNEAN SOCIETY, and the honorary degrees of D.Sc. from CAMBRIDGE and D.C.L. from OXFORD.

He became a Fellow of the ROYAL SOCIETY in 1856 and was a Member of its Council for four periods of one to two years each; a member of the ROYAL GEOGRAPHICAL SOCIETY (1853) and for many years a member of its Council; three time Sectional President of the BRITISH ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE,—Geography 1872, Anthropology 1877, 1885,—General Secretary 1863-1867, and twice declined the Presidency; a member of the METEOROLOGICAL COMMITTEE; Chairman of the KEW OBSERVATORY COMMITTEE; President of the ANTHROPOLOGICAL INSTITUTE; Rede Lecturer at CAMBRIDGE 1884, and Herbert Spencer Lecturer at OXFORD 1907.

The diversity of the honors conferred upon him bears testimony to the intellectual versatility of the man and to the power of his personality. His "Memories of my life," published in 1908, furnishes not merely a charmingly written account of his own life activities, but affords the thoughtful reader some insight into the great advance of science during the life of one individual. Summing up FRANCIS GALTON's own work in a single phrase, his greatest contribution to science during his long life was his influence for the quantification of method. This influence is nowise diminishing with the lapse of time, and must long be felt in many fields of scientific activity.

A comprehensive biography, one volume of which appeared in 1914 from the Cambridge University Press, is in preparation by Professor KARL PEARSON, the first incumbent of the GALTON PROFESSORSHIP OF EUGENICS.

The portrait here reproduced was one of the last works of CHARLES WELLINGTON FURZE (1868-1904), who achieved in his brief life a high place among British portrait painters. A copy by CARTER is hung in Trinity Hall, CAMBRIDGE. The original is in the possession of Sir FRANCIS GALTON's nephew, E. WHEELER GALTON, Esq., Claverdon Leys, Warwick, England, who has kindly given his consent to its reproduction in GENETICS.

GENETICS is indebted to Mr. W. E. L. STOKES, well known horsebreeder, of New York City, and author of *"The right to be well born,"* for generously providing the funds required for the reproduction of this portrait.

GENETICAL STUDIES OF VARIEGATED PERICARP IN MAIZE[1]

R. A. EMERSON
Cornell University, Ithaca, N. Y.

[Received July 24, 1916]

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PREVIOUS STUDIES

Two years ago there were presented some results of a study of the inheritance of self pattern in the pericarp of maize seeds, occurring as a sporophytic[2] variation in variegated ears (EMERSON 1914). Further results, in entire accord with those previously reported, have now been obtained. In addition, data bearing upon new phases of the problem are also available.

The chief results reported in the earlier paper were the following: (1) The more nearly self-colored the pericarp of any seed of a variegated ear, the more likely is the progeny of that seed to produce a self-colored

[1] Paper No. 55, Department of Plant Breeding, Cornell University, Ithaca, N. Y. Most of the data here reported were obtained in connection with heredity studies conducted at the Nebraska Agricultural Experiment Station and supported by funds of that institution.

[2] This change has heretofore been termed somatic variation because first manifested in somatic cells. As was apparent from the start, however, the factorial modification responsible for the visible change must often occur in meristematic cells from which later arise the germ cells as well as the somatic tissues of the pericarp or even of the whole ear. Since such meristematic cells—progenitors of epidermal tissue being excluded—are germinal rather than somatic, the variation is better termed sporophytic.

ear and the less likely to produce a variegated or colorless one. (2) Self-colored ears so produced behave as if they were F_1 hybrids between self-colored and variegated or between self-colored and colorless races, depending upon whether the variegated parent ear was homozygous or heterozygous for pericarp color and upon whether it had been self- or cross-pollinated. (3) Self-colored ears also occur occasionally with the normal variegated ears in F_1 of a cross produced by pollinating a colorless race with pollen from a variegated race; and these F_1 red ears always behave in later generations as if they were hybrids between self-colored and colorless races.

As a possible interpretation of these results, I have suggested (1) that a Mendelian factor for variegation, *V*, is changed to a self-color factor, *S*, in a meristematic cell, (2) that all pericarp cells directly descended from this modified cell develop color, (3) that of the female gametes arising from such modified cells at least one-half carry the *S* factor in place of the *V* factor, and (4) that a similar factorial change is responsible for the occasional occurrence of male gametes bearing *S* instead of *V*. It was also noted in the former paper that a certain dark variegation occurring in association with a self-colored cob spot was apparently not inherited, but that, nevertheless, distinctly different types of variegation exist in an apparently homozygous condition in different strains of maize.

MATERIALS AND METHODS, SOURCES OF ERROR

Most of the data reported in my first paper were obtained from self-pollinated ears. As was there pointed out, such data are not wholly reliable for the reason that factorial changes influencing the male gametes are never detected in the staminate inflorescence. Assurance that the pollen is not carrying a factor for self color is to be had only when pollen from colorless races is employed. In all the work done since the earlier publication, therefore, seeds have been selected only from variegated ears that had been pollinated by races with colorless pericarp.

Since on the great majority of variegated ears only a few self-colored or nearly self-colored seeds occur, and since variegated ears with a considerable number of such seeds are rare, a large number of ears must be crossed in order to get a sufficient number of self-colored seeds to afford reliable indications. To hand-pollinate a sufficient number of ears for this purpose was found impracticable owing to the short period during which the work could be done and the considerable amount of time necessarily devoted to pollination in connection with other maize studies. Cross-pollination was therefore effected by detasseling all

plants grown from variegated seed and allowing them to be pollinated naturally from colorless races grown in alternate rows. The plan followed was to examine all the plants once every day and to remove all tassels as soon as they began to show above the sheaths. This work was done by careful assistants under my direction throughout the blossoming period.

In work conducted in this way, two sources of error should be noted: (1) There is a chance that a few tassels may be overlooked until after they have begun to shed pollen. (2) A few of the pollinizers may not be colorless. As to the first of these, it can be said that no open anthers were found on any tassel of the detasseled rows and that therefore, even if such occurred, the error introduced by them was probably not greater than would have resulted from the accidental entrance of foreign pollen in guarded hand-pollination.

The second source of error, on the other hand, was positively demonstrated. Of about 1000 plants in the pollinizer rows, a single plant had self red ears. Owing to the extremely unfavorable season (1913) numerous plants with fairly well developed tassels failed to produce ears. Unfortunately, therefore, it cannot be said that the single red-eared plant observed was the only one of the sort present. In fact there is reason to believe that it was not the only off-type plant present by accident, as will appear shortly. Since there was almost no chance that the colorless seeds planted could have contained any colored seeds or that such seeds were accidentally scattered in the field, it is probable that the red-eared plant was due to an accidental admixture of pollen when the parent ear was hand-pollinated the summer before.

If hand-pollination had been practiced in this investigation and pollen accidentally taken from a red-eared plant, the ears so crossed could have been discarded. In open pollination, however, it obviously could not be determined which ears had received pollen from the off-type plant. Unfortunately, I may add carelessly, the detasseled rows were harvested before the pollinizers were and consequently before the red-eared plant was discovered. It was, therefore, impossible even to discard seed ears grown near the red-eared plant.

The only method of determining how serious such accidental admixture of pollen might be was to grow progenies of colorless ears from the pollinizer rows. In order that this test might give a fair indication of the amount of off-type pollen, numerous colorless ears were taken at random from each pollinizer row and about twenty seeds from each ear were planted in 1914. In all 134 such colorless parent ears were

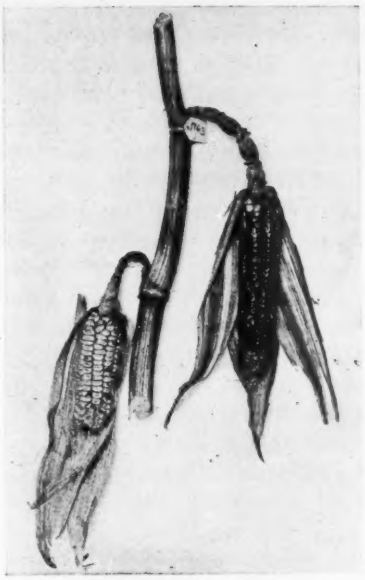
represented in the planting. Owing to poor germination only 1239 plants resulted. Of these one plant had self-colored ears and five had variegated ears—an error due to off-type pollen of about one half of one percent. The five variegated ears could not have come from pollen of the one red-eared plant observed, for the progeny of this plant had only self-colored and colorless ears. Pollen carrying the variegation factor must therefore have come from some other plant or plants in the pollinizer rows or from the detasseled rows. The percentage of error is so small, however, that it need occasion little difficulty.

Many of the pollinizers that were colorless with respect to pericarp had self red cobs. This fact introduces a difficulty in connection with a study of the inheritance of a peculiar form of dark variegation associated with red cob color. The matter will be considered in its appropriate place later.

TYPES OF SEED COLOR AND OF EAR COLOR

From every variegated ear used in the next season's planting, seeds of as many types of pericarp color as possible were chosen. Each type from each ear was planted separately. Almost no wholly self-colored seeds were found. In practically all cases the most nearly self-colored seeds had colorless or extremely light colored crowns. These light crowns appear as if made up of very narrow light streaks extending from part way down the side of the seeds opposite the germ up to and converging at the point of attachment of the silks to form irregular light spots (figures 1 and 2 B). Even when these grains occurred in large patches on "freak" ears, almost no wholly self-colored seeds appeared. The cob color under such "near self" seeds, whether they occurred singly or in patches of considerable size, was rarely prominently different from that of the remainder of the ear. That is, the cobs were, as a rule, variegated throughout. Under patches of near self seeds, the color of the cob was ordinarily only slightly darker than elsewhere, the change being due to a somewhat uniform development of color at the base of the glumes (figure 3 C, D).

In addition to numerous fine and often somewhat indistinct longitudinal lines of color characteristic of most variegated maize seeds, some seeds have one or more sharply defined and deeply colored stripes (figure 4). A single stripe may cover anywhere from perhaps one twenty-fifth to nine-tenths, or more, of the seed. The stripe is always self-colored, not broken by lighter variegations. Seeds in which these self-colored stripes cover from above 50 percent to 90 percent, or more,



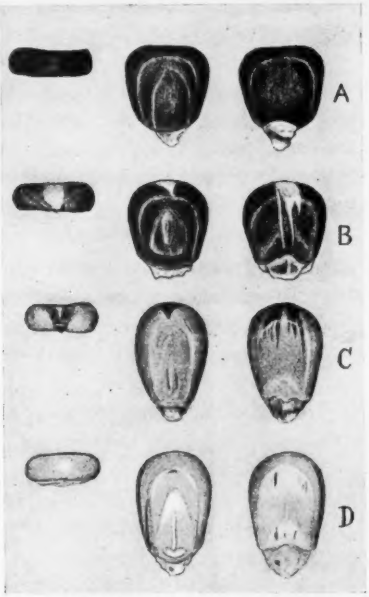


FIGURE 1.—Very light variegated type of maize with one normal ear (left) and one "freak" ear (right), the latter made up of self-colored and near self seeds except for three very light variegated ones near the shank. Note also the striped husks. From photograph by W. I. FISHER.

FIGURE 2.—Types of maize seeds, crown (left), germ side (middle), and side opposite germ (right). A, self-colored, B, near self, C, dark-crown variegated, D, very light variegated. Note the similarity in color pattern of B and C. From drawings by C. W. REDWOOD.

of the area, are classed together as "more than half self" (figure 4 B). Similarly seeds with a stripe covering from about 10 percent to somewhat less than 50 percent are designated as "less than half self" (figure 4 C).

The next most highly colored seeds are known as "dark-crown variegated." These are usually rather evenly variegated, with dark crowns. On all sides of the seed there is usually a rather prominent light red color (brown in some strains) forming a background for the fine lines of darker color that make up the variegation. On the side of the seed opposite the germ are prominent stripes that converge at the point of attachment of the silks to form an irregular, dark crown spot (figures

2 C and 4 D). These dark-crown seeds are almost the exact reverse of the "near self" seeds described above, in that the light pattern of one is the counterpart of the dark pattern of the other. These dark-crown variegated seeds almost if not quite universally occur above a self-colored (red or brownish) spot of the cob. This is apparently equally true whether these seeds occur singly or in "freak" patches. In the latter case the exact correspondence in outline between cob and seed patches is most striking (figure 3 A, B). This is the only type of variegation that is commonly thus associated with dark color in the cob. In earlier statements (EMERSON 1913, 1914), I have spoken of an association between self-colored or near self seeds and self-colored cob spots, but I now believe that such an association is rarely if ever found.

Most variegated maize seeds lack the dark crown spot of seeds of the

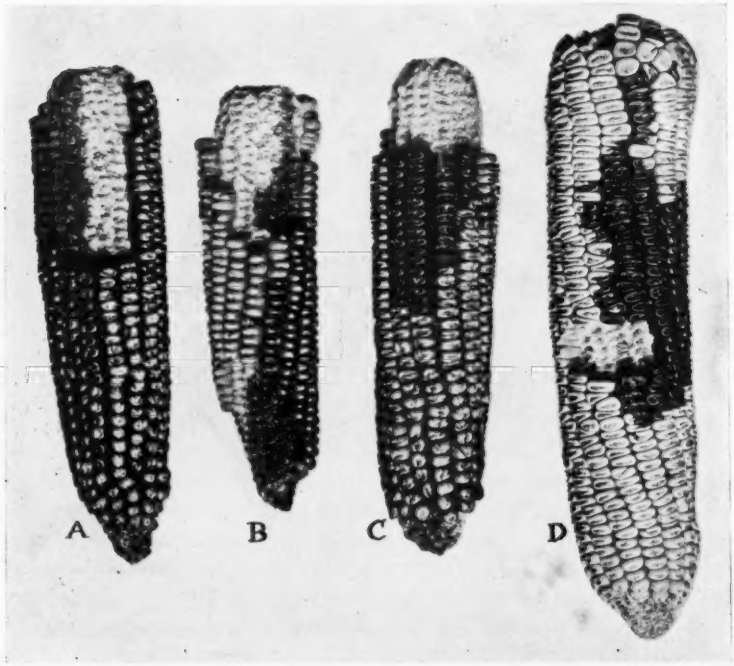


FIGURE 3.—Medium (A, C) and very light (B, D) variegated ears with "freak patches" of dark-crown (A, B) and near self (C, D) seeds. Note the association of self-colored cob spots with patches of dark-crown seeds. From photograph by W. I. FISHER.

dark-crown variegated type described above, and usually also show little or none of the light red (or brown) background noted in connection with that type. Such seeds are here known as "medium variegated" (figure 4 E). A still lighter type is distinguished as "light variegated" (figure 4 F). These differ from medium variegated seeds in degree only. They have fewer of the dark lines forming the variegation.

Still another class is known as "very light variegated." Except for occasional very narrow longitudinal lines, these seeds are almost colorless (figure 4 G). While such seeds are found occasionally on medium variegated ears, they are characteristic of certain strains of variegated maize. At a distance the ears of these strains appear colorless. Most of the seeds, however, have from one to several minute streaks or specks of color. Very light variegated ears often contain a few seeds with wholly colorless pericarp (figure 4 H).

The classes of ears are similar in part to the classes of seeds described above. Thus, I have recognized self-colored, dark, medium, light, and very light, variegated, and colorless, ears. Self-colored ears (red or brown) unlike the self and near self seeds of the variegated ears, always (so far as I have observed) have self-colored (red or brownish) cobs. In certain families a number of almost wholly self-colored ears have been observed. They are exactly like the self-colored ears in seed and cob color except that from one to at the most four or five scattered seeds are distinctly variegated. Such ears are not to be confused with the "near self" seeds described above, for their seeds, except for the very few variegated ones, are wholly self-colored. They never show the light or colorless crown spots of near self seeds. Only one ear composed almost wholly of near self seeds has ever been observed by me, and it was doubtless a "freak" ear in which the patch of near self seeds extended over nearly the whole ear instead of being confined to a smaller patch associated in the usual way with variegated grains. The ear in question not only had a light variegated cob but was borne on the same stalk with an ordinary light variegated ear (figure 1).

Ears the individual seeds of which are, throughout, say a quarter or a half self-colored, are never seen. Dark-crown variegated ears, composed wholly of dark-crown seeds, are rarely found. The three or four observed have had wholly self-colored (red) cobs. They are, I believe, to be regarded as "freak" ears, in which the patch of dark-crown seeds happened to extend over the entire ear. One such ear has been found on the same stalk with a medium variegated ear, the latter having as usual a variegated cob.

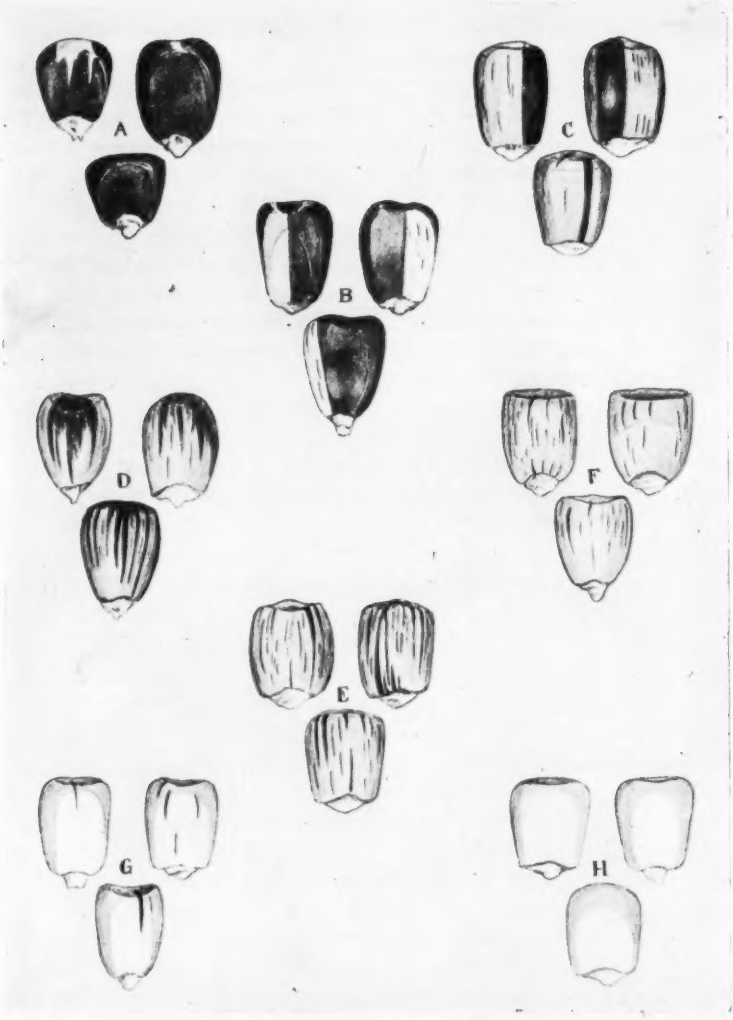


FIGURE 4.—Types of maize seeds selected from variegated ears for planting, as indicated in tables 1 and 3. A, self-colored and near self, B, more than half self, C, less than half self, D, dark-crown variegated, E, medium variegated, F, light variegated, G, very light variegated, H, colorless. From drawing by C. W. REDWOOD.

Medium variegated ears, composed in the main of medium variegated seeds but usually with scattered half self, quarter self, near self, or dark-crown seeds, and rarely freak patches of near self or dark-crown seeds, are very common (figure 3 A, C). If homozygous for variegated pericarp, they apparently always have variegated cobs. When crossed with strains having colorless pericarp and self red cobs, the resulting F_1 ears are variegated with red cobs and in F_2 all the variegated ears with red cobs are heterozygous and all with variegated cobs are homozygous for both pericarp and cob colors. Light variegated ears are like the above except that most of their grains are light variegated. Just as with medium and light variegated seeds, no sharp line of demarkation exists between medium and light variegated ears. While some ears are clearly much lighter than others, numerous intermediates are usually found in the same lots.

Very light variegated ears are composed mostly of very light variegated and colorless seeds. They rarely produce self-colored, near self, or dark-crown seeds, and I have observed among them only a few "freak" ears with large patches of dark-crown or near self seeds (figure 3 B, D). In this respect they differ notably from medium variegated ears. Their cobs are very light variegated or nearly colorless, except, as in the case of medium variegated ears, when they have been crossed with colorless-seeded, red-cobbed types, in which case all heterozygous ears have red cobs. Some apparently wholly colorless ears have been observed in strains of very light variegated maize and are doubtless to be regarded as an extreme expression of this type of variegation. Self-pollinated seeds of one such ear were found to yield a progeny consisting mainly of very light variegated ears. Very light variegation is recessive to medium variegation, as will be shown later, and the two types segregate rather sharply in F_2.

INHERITANCE OF SPOROPHYTIC MUTATIONS FROM VARIEGATION TO SELF COLOR

The variegated ears, cross-pollinated by plants with colorless pericarp, as noted earlier in this paper, may be divided into two general lots, one of which was homozygous with respect to pericarp color and the other of which was heterozygous from having been crossed with colorless maize the previous generation. A part of the homozygous variegated lot was in reality heterozygous for medium and very light variegation.

Of the lot that was heterozygous for variegated pericarp, seeds of various color types were selected from seventy-five parent ears, and

progenies totaling 1140 plants were grown. Since we are here concerned with the inheritance of self color as contrasted with variegation, all the variegated ears will be lumped together without respect to the type of variegation. The numbers of self-colored, variegated, and colorless ears produced by the various types of seeds are given in table 1.

Since the parent ears were heterozygous for pericarp color and were cross-pollinated by colorless maize, fifty percent of the progeny of each class of seeds should have been colorless. The percentages of plants with colorless ears actually observed ranged from a little less than 46 to a little over 62. The percentage of colorless ears in the lot as a whole was 50.96. It seems likely that the individual deviations from the expected 50 percent are without significance. There is certainly no regular tendency toward either an increase or a decrease in the percentage of colorless ears from the self-colored seed to the lighter variegated seed. It can be concluded therefore that these data afford no evidence of any effect of the amount of color in the seeds of heterozygous variegated ears upon the relative numbers of colored and colorless offspring.

The things that stand out most prominently in these results are, (1) the direct relation between the amount of self color in the seeds planted and the percentage of plants with self-colored ears in the progenies in the first three classes; (2) the lack of any such relation between the amount of color in the seeds and the percentage of self-colored ears produced from the various classes of variegated seeds; and (3) the entire absence of variegated ears in the progeny of self-colored and near self seeds.

It seems likely that the difference in percentages of self-colored ears from the several classes of variegated seeds is without significance. Only a single self-colored ear appeared in the progeny of any one class of these seeds. It is perhaps, however, significant that no regular increase in self-colored ears appears as we pass from the very light variegated seeds with very little color, to the dark-crown variegated seeds which have considerable color, particularly at the crown. The possible significance of this fact will be considered later.

The percentages of self-colored ears in the plants grown from self or near self seeds, from more than half self seeds, from less than half self seeds, from variegated seeds (all classes of the latter being lumped together), and from colorless seeds, approximately 51.1, 27.5, 6.9, 0.3 and 0, respectively, are similar to the percentages calculated from results previously reported (EMERSON 1914). The combined results, including all data now available, are brought together in table 2.

TABLE I

Progenies of different classes of maize seeds from seventy-five heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants				Percentages		
	Self-colored ears	Variegated ears	Colorless ears	Total	Self-colored ears	Variegated ears	Colorless ears
Self and near self	23	—	22	45	51.11	——	48.89
More than half self	14	5	32	51	27.45	9.81	62.74
Less than half self	6	38	43	87	6.90	43.68	49.42
Dark-crown variegated	—	91	78	169	——	53.85	46.15
Medium variegated	1	159	209	369	.27	43.09	56.64
Light variegated	1	48	41	90	1.11	53.33	45.56
Very light variegated	1	141	125	267	.37	52.81	46.82
Colorless	—	31	31	62	——	50.00	50.00
Total	559		581	1140	49.04		50.96

TABLE 2

Progenies of different classes of maize seeds from heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants				Percentages		
	Self-colored ears	Variegated ears	Colorless ears	Total	Self-colored ears	Variegated ears	Colorless ears
Self and near self.....	37	—	36	73	50.68	——	49.32
More than half self.....	18	7	34	59	30.51	11.86	57.63
Less than half self.....	9	43	52	104	8.65	41.35	50.00
Variegated	10	704	754	1468	.68	47.96	51.36
Colorless	—	58	51	109	——	53.21	46.79
Total	886		927	1813	48.87		51.13

That the percentage of self-colored ears in the progeny is roughly proportional to the amount of self color in the seeds planted is evident. Since the parent ears were heterozygous for variegated pericarp, the *V* factor was simplex. On the basis of the hypothesis advanced in my former paper, if this single *V* factor is changed to an *S* factor early enough so that the whole pericarp is self-colored, the gamete concerned is assumed always to arise from a modified cell containing *S* instead of *V*. Since *V*, from which *S* came, was simplex, *S* will also be simplex. Half the gametes formed in connection with self-colored seeds will, therefore, carry *S* and half will carry a factor for colorless pericarp, so that half the plants resulting from such self-colored seeds should have self-colored ears and half colorless ears. This expectation has been almost exactly realized.

If the seeds that are classed here as more than half self-colored are assumed to average 75 percent self and those classed as less than half self-colored are assumed to average 25 percent self, the percentages of plants with self-colored ears expected from them are 37.5 and 12.5 respectively. The percentages actually observed were 30.51 and 8.65 respectively, a sufficiently close approximation to expectation when allowance is made for the fact that the seeds planted may not have averaged 75 percent and 25 percent as assumed.

Perhaps the most striking feature of these results is the total lack of variegated ears in the progeny of self and near self seeds. This is in exact accord with expectation, since if a simplex *V* mutates to an *S*, *V* could be present in no gamete associated with a self-colored seed. The number of plants from self-colored seeds in table 2 is small, to be sure, totaling only 73. It is permissible, however, to add to this number the records of HARTLEY (1902), of EAST and HAYES (1911, pp. 106-107) and of my own open-pollinated cultures (EMERSON 1914), since the parent ears in all these cases were obviously heterozygous for variegated pericarp and were presumably pollinated from colorless plants. Combining all these lots, we have from self and near self seeds 186 plants with self-colored ears, 177 with colorless ears, and not a single plant with variegated ears.

A noteworthy point in connection with this result is that many, doubtless most, of the seeds planted were not wholly self-colored but were what are here called near self, that is, they had a small colorless or nearly colorless spot at the crown. It will be recalled that the dark-crown variegated seeds (table 1) produced no self-colored ears though they are characterized by dark colored crowns corresponding almost exactly

to the light crowns of the near self seeds. It would appear, therefore, that there is no connection between the color at the crown of the seed and the production of self-colored ears in the next generation.

We have now to consider the behavior of variously colored seeds from homozygous variegated parent ears. All these ears were cross-pollinated by colorless maize just as were the heterozygous ears considered heretofore. Seeds of various color types were selected from 80 homozygous variegated ears and a total of 1972 plants grown from them. The results are recorded in table 3.

TABLE 3

Progenies of different classes of maize seeds from eighty homozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Progenies				
	Number of plants			Percentages	
	Self-colored ears	Variegated ears	Total	Self-colored ears	Variegated ears
Self and near self.....	71	72	143	49.65	50.35
More than half self....	43	67	110	39.09	60.91
Less than half self.....	16	150	166	9.64	90.36
Dark-crown variegated..	1	528	529	.19	99.81
Medium variegated.....	2	607	609	.33	99.67
Light variegated.....	2	125	127	1.57	98.43
Very light variegated...	1	269	270	.37	99.63
Colorless	—	18	18	——	100.00

Here, just as with the heterozygous variegated parent ears, the several classes of variegated seeds showed no regular difference as to the percentage of self-colored ears produced. The considerable amount of color at the crown of dark-crown variegated seeds, as noted before, has no apparent relation to the production of self-colored ears in the progeny.

The percentages of plants with self-colored ears from the five classes of seeds—self or near self, more than half self, less than half self, variegated (all classes together), and colorless—are not far different from the percentages found in case of heterozygous parent ears, as can be seen from the following comparison (table 4).

The important point here is that, when the variegation factor is duplex, the percentage of self-colored ears in the offspring is not greater than when that factor is simplex. This indicates that ordinarily only one

TABLE 4

Self-colored ears in progenies of different classes of seeds from homozygous and heterozygous variegated ears cross-pollinated by colorless maize.

Seeds planted	Percentage of self-colored ears	
	Homozygous parents	Heterozygous parents
Self and near self.....	49.65	50.68
More than half self.....	39.09	30.51
Less than half self.....	9.64	8.65
Variegated	.39	.68
Colorless	0	0

of the duplex factors of a sporophytic cell mutates. That is, *VV* becomes *VS* not *SS*. Both *V* factors may at times change to *S* factors, but such is not the case frequently enough to affect materially the percentage of self-colored ears and no test other than percentage differences is available. This question has been discussed elsewhere (EMERSON 1913).

Since only one of the duplex *V* factors ordinarily changes to an *S* factor in any one sporophytic cell, and if one *V* factor mutates as readily as the other, it follows that on the average about twice as many self-colored seeds should be found on homozygous as on heterozygous variegated ears. The same difference should be noted in the progenies of non-colored maize when cross-pollinated by homozygous and heterozygous variegated-eared plants. Attention is being given to this matter at the present time.

As noted earlier in this discussion, some of the ears classed above as homozygous were in reality the result of a cross of two distinct strains of variegated maize, one medium variegated and the other very light variegated. While there is some variation in both of these strains, particularly in the medium variegated one, some ears having more color than others, there is no overlapping between them. Ears of the very light variegated strain often appear colorless until examined somewhat closely. A single cross between this strain and a self-colored strain gave sharp segregation in F_2 into self-colored and very light variegated ears with none medium variegated. Numerous crosses of medium variegated with self-colored strains have likewise thrown self-colored and medium variegated offspring with no very light variegated ears. Self color is dominant to both types of variegation. Finally, crosses between the two

variegated strains have shown medium variegation to be dominant to very light variegation in F_1 and have resulted in simple Mendelian segregation in F_2.

Both medium variegated and very light variegated strains have occasional seeds that are self-colored, near self, half self, etc., though this is much less common in the very light variegated strain than in the medium variegated one. The F_1 medium variegated ears from the cross of the two strains also, of course, have some such seeds. A study of the progeny of the several classes of seeds from thirty of these F_1 variegated ears, a total of 747 plants, has given important results of a kind not heretofore reported. They are brought together in table 5.

The important features of these records are: (1) The percentage of plants with very light variegated ears was not greater when the seeds planted were very light variegated than when they were medium and dark-crown variegated. From all classes of variegated seeds together, approximately 49 percent of the offspring were medium variegated and 51 percent very light variegated, where 50 percent of each was to have been expected. (2) The percentage of self-colored ears was roughly proportional to the amount of self color in the seeds planted. The deficiency of self-colored ears below the expected 50 percent from near self seeds is probably without significance, being due most likely to the small numbers involved. (3) The percentage of medium variegated ears decreased as the percentage of self-colored ones increased. Evidently, the self-colored ears were produced at the expense of medium variegated ears and not at the expense of very light variegated ones.

The significance of this is that in these F_1 plants the factor for medium variegation mutates much more frequently than the factor for very light variegation,—V_mV_l ordinarily becomes SV_l rather than V_mS. This is to be expected from the fact that self-colored and near self seeds occur much less frequently on very light variegated ears than on medium variegated ones. Whether V_mV_l ever becomes V_mS cannot now be said for no evidence is available. This probably does occur, however, for there is abundant evidence that V_lV_l does occasionally, though rarely, become V_lS.

CHANGES IN TYPE OF VARIEGATION

Both medium and very light variegated ears of maize are quite as likely to exhibit pronounced sporophytic variations to dark-crown variegation as to self color. The dark crown spots of these seeds make a "freak patch," or even a single seed, to stand out from the normally

TABLE 5

Progenies of different classes of seeds from thirty F_1 variegated ears of a cross between medium variegated and very light variegated strains, pollinated by colorless maize.

Seeds planted	Progenies						
	Number of plants				Percentages		
	Self-colored ears	Medium variegated ears	Very light variegated ears	Total	Self-colored ears	Medium variegated ears	Very light variegated ears
Self and near self.....	16	—	27	43	37.21	——	62.79
More than half self.....	16	7	31	54	29.63	12.96	57.41
Less than half self.....	8	25	35	68	11.76	36.77	51.47
Dark-crown variegated	—	92	108	200	——	46.00	54.00
Medium variegated	—	102	104	206	——	49.51	50.49
Very light variegated	—	91	85	176	——	51.70	48.30
Total	40	317	390	747	5.35	42.44	52.21

colored seeds of the same ear almost as strikingly as does a patch of near self seeds. The fact that dark-crown variegated seeds are almost if not quite universally underlaid by a self-colored cob patch corresponding accurately in outline to the patch of seeds with dark crowns adds not a little to the distinctiveness of this sporophytic variation (figure 3 A, B). In my first paper (EMERSON 1914), it was noted that there was then no evidence of the inheritance of this variation. The same statement might suffice even at present, but the evidence against such inheritance is now so strong that it seems important to present it here, if for no other reason than to emphasize a surprising difference between two almost equally striking sporophytic variations that often occur on the same ear.

Occasionally an ear is found to be divided sharply into two parts, one consisting of seeds that show the ordinary medium-variegation pattern and the other of seeds that are light variegated. Such variations have been much less common in my material than the occurrence of dark-crown variegated and near self seeds. In addition to these very distinct variations, many medium variegated ears have some grains showing all gradations from medium to light or very light variegation.

Of all the instances of sporophytic change in type of variegation that I have investigated, only a few afford any indication of having reached the germ plasm. All these occurred in a single lot of maize. A medium variegated ear with variegated cob, cross-pollinated by a strain of maize with colorless grains and self-colored cobs, produced both medium variegated and very light variegated offspring, all, of course, with self-colored cobs. The parent was, therefore, heterozygous for the two types of variegation. Since it was pollinated by colorless maize, both types of offspring must have been heterozygous, the one for medium variegation and the other for very light variegation. If V_m and V_l are allelomorphic, as there is every reason to believe, no ear could have contained both of these factors. An ear of this lot with medium variegated grains and red cob was self-pollinated and next generation gave colorless ears with self-colored cobs, medium variegated ears with self-colored cobs, and medium variegated ears with variegated cobs, in a ratio approximating 1 : 2 : 1, as was expected of it. No light variegated ears were noted and, of course, none were expected. Since self color of cob is allelomorphic to variegated color of grains, the ears with self-colored cobs were obviously heterozygous for pericarp color as well as for cob color and those with variegated cobs were homozygous. The latter may, therefore, be designated as V_mV_m. Three of these homozygous medium

variegated ears had more or less distinct "freak" patches of rather light variegated seeds. The two classes of seeds from these three ears were planted separately with the following results (table 6).

TABLE 6

Progenies of medium variegated and light variegated seeds of homozygous medium variegated parent ears cross-pollinated by colorless maize.

Seeds planted	Number of plants		
	Medium variegated ears	Light variegated ears	Very light variegated ears
Medium variegated	64	12	0
Light variegated	41	10	18

The ears recorded as medium variegated and light variegated respectively were not sharply separable on account of numerous intermediates and should possibly have been classed together. The very light variegated ears, on the other hand, were a fairly uniform lot and were distinctly lighter than the lightest of the ears classed as light variegated. The striking feature of these records is the fact that no very light variegated ears were produced from medium variegated seeds, while from the light variegated seeds of the same parent ears there were 18 plants, about 26 percent of the total number, with very light variegated ears.

Upon the behavior of such very light variegated ears in later generations will depend the answer to the question whether they are true mutations. Until such tests can be made, it is perhaps idle to speculate about the possible manner of their origin. There are two features of the result, however, that deserve comment. We know that the parent ears were V_mV_m and that they were pollinated by colorless maize. If it be assumed that the very light variegated ears arose through a change of V_m to V_l,—the only assumption that seems at all reasonable,—how can we explain the visible somatic modification, and how account for the fact that only about 26 percent rather than 50 percent of the ears from the light colored seeds were very light variegated?

If V_mV_m change to V_lV_l, the seeds should be very light variegated, but in that case 100 percent of the progeny should be very light variegated. If V_mV_m becomes V_mV_l, 50 percent of the offspring should be very light variegated but the parent seeds themselves should not have been affected,

since medium variegation has been found to be dominant to very light variegation. As a matter of fact my descriptions, made, of course, the year before these results were obtained, indicate that the parent seeds were not what I have termed very light variegated, but were merely sufficiently lighter than the medium variegated seeds of the same ears to be readily detected when found in solid patches on those ears. Perhaps medium variegation is not always completely dominant over very light variegation. This, however, since I have not noted partial dominance in actual crosses between these types, is so obviously an attempt to make the facts fit the hypothesis that the matter had best be dismissed with the mere statement that the record presented here is the only evidence, slight as it is, that a sporophytic change in type of variegation of maize pericarp is ever of the nature of a true mutation.

From various other ears both homozygous and heterozygous for medium variegated pericarp, light and very light variegated seeds scattered over the ears have been selected and have given no evidence of the inheritance of the type of variegation shown by them. The available data are given in table 7. The records are grouped so that parent ears of like nature, homozygotes or heterozygotes, are classed together.

From many of the same parent ears employed for the comparison given in table 7 and from some others, ninety-one in all, dark-crown variegated seeds were selected for planting in comparison with medium variegated seeds of the same ears. The data obtained from these tests are given in table 8.

It is obvious that, so far as the available data go, they give no indication that dark-crown variegation occurring as a sporophytic variation is ever inherited. This behavior is noteworthy in contrast to the definite inheritance of self or near self color when it occurs as a sporophytic variation in variegated maize—the more particularly so because the visible change is quite as definite and almost as striking in the one case as in the other. The cause of this difference is reserved for discussion later in this paper.

The possible inheritance of self color of the cob, which occurs as a sporophytic variation, so far as I have observed, universally associated with dark-crown variegated seeds on otherwise variegated cobs, is of even more interest than the inheritance of variations in pericarp color. Dark-crown variegation of maize seeds does not, so far as I am aware, exist except as a sporophytic variation, while self color of the cob is always associated with the more common self colors of the pericarp,

TABLE 7

Progenies of light variegated and of medium variegated seeds from seventy-two homozygous and heterozygous variegated ears.

Seeds planted	Progenies						
	Number of plants					Percentage	
	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total	Light variegated ears	Very light variegated ears
Twenty-one ears—							
Medium variegated....	118	7	—	—	125	5.60	—
Light to very light variegated	111	6	—	—	117	5.13	—
Twenty-four ears—							
Medium variegated....	82	8	—	98	188	4.26	—
Light to very light variegated	27	3	—	24	54	5.56	—
Twenty-seven ears—							
Medium variegated....	122	8	167	—	297	2.70	56.23
Light to very light variegated	44	4	49	—	97	4.12	50.52

TABLE 8

Progenies of dark-crown variegated and of medium variegated seeds from ninety-one homozygous and heterozygous variegated ears.

Seeds planted	Progenies								
	Number of plants						Percentage		
	Dark-crown variegated ears	Medium variegated ears	Light variegated ears	Very light variegated ears	Colorless ears	Total	Dark-crown variegated ears	Light variegated ears	Very light variegated ears
Twenty-seven ears—									
Medium variegated....	—	243	9	—	—	252	—	3.57	——
Dark-crown variegated	—	200	1	—	1	202	—	.50	——
Thirty-seven ears—									
Medium variegated....	—	76	9	—	114	199	—	4.52	——
Dark-crown variegated	—	64	4	2	60	130	—	3.08	1.54
Twenty-seven ears—									
Medium variegated....	1	134	9	141	—	285	.35	3.16	49.47
Dark-crown variegated	—	70	3	91	—	164	—	1.83	55.49

dark red and dark brown, and is frequently found in strains with colorless pericarp.

Unfortunately, the occurrence of self-colored cobs in the progeny of dark-crown variegated seeds cannot in these studies be taken as an indication of the inheritance of a sporophytic variation in cob color, for the reason that a considerable number of the plants used as pollinizers, though colorless as regards pericarp, had self-colored cobs. A part of the progeny of all seed classes was, therefore, expected to have self-colored cobs, so that the only criterion of the inheritance of sporophytic variation to self color in cobs is the relative percentages of plants with self-colored cobs in the progenies of dark-crown variegated and of medium variegated seeds.

Of the 1057 plants with variegated ears listed in table 8, 435 came from dark-crown seeds all of which were associated definitely with self-colored patches of the otherwise variegated cobs to which they were attached, while 622 grew from medium variegated seeds associated with variegated cob patches of the same ears. All these plants with variegated ears had variegated cobs except 60 of those from dark-crown seeds and 88 of those from medium variegated seeds. The percentages of plants with self-colored cobs were, therefore, about 13.8 for the progeny of dark-crown seeds and about 14.2 for the progeny of medium variegated seeds. Of 1486 plants grown from seed of the plants with colorless pericarp and colorless cobs used as pollinizers, 208, or almost exactly 14 percent, had self-colored cobs. There is certainly nothing in these results to indicate that a sporophytic variation from variegation to self color of the cob is inherited.

REVERSE MUTATION—SELF COLOR TO VARIEGATION

In certain cultures of maize there have been noted ears that are self-colored except for a single variegated grain or a grain that is half variegated and half self, one-third variegated and two-thirds self, etc. Frequently, two or three and in a few cases as many as five such grains have been found on a single otherwise wholly self-colored ear. In the records presented earlier in this paper all such ears have been listed as self-colored, and I think rightly so, just as ears that were variegated throughout except for a few self-colored seeds have been listed as variegated. In short, I regard the occurrence of these variegated seeds on self-colored ears as due to sporophytic mutations from self color to variegation. I must admit, however, that there is at present very little direct evidence as to the real nature of these variegated seeds.

Few such variegated seeds have been tested and most of these have not been wholly desirable material for the tests. The seeds tested were found mainly on ears that were heterozygous for self-colored and variegated pericarp, *SV*. Even the self-colored seeds of these ears should throw 25 percent or 50 percent variegated ears the next generation, the actual percent depending, of course, upon whether the parent ear was self-pollinated or crossed by colorless maize. If the *S* factor of such an ear change to *V* the result would be to produce homozygous *VV* tissue. Any seed in the modified part of the ear would be variegated. But collectively such seeds would produce only 50 percent of variegated offspring if self-pollinated, because half the pollen would carry dominant *S*, and 100 percent variegated if crossed by colorless maize. The only criterion of the assumed mutation is, therefore, a difference in percentages of variegated offspring from the self-colored and variegated seeds of the same ear. This would be fairly conclusive if larger numbers could be dealt with, but since the numbers that can be grown are small owing to the rarity of such variegated seeds, the results are not satisfactory.

Self-colored ears that are heterozygous for self-colored and colorless pericarp afford satisfactory material but as yet I have been unable to take full advantage of it. Half the gametes of such a plant ordinarily carry the *S* factor and the other half carry a factor for colorless pericarp. If then *S* become *V* in connection with variegated grains and if the ear were cross-pollinated by colorless maize, the variegated seeds should throw 50 percent variegated and 50 percent colorless offspring while the self-colored seeds should throw 50 percent self-colored and 50 percent colorless offspring. The failure of self-colored seeds to produce variegated ears and of variegated seeds to produce self-colored ears would furnish definite evidence of a factorial change. Large numbers would not, therefore, be required.

If, on the other hand, this self-colored ear, heterozygous for pericarp color, were self-pollinated, the self-colored seeds would, of course, throw 75 percent self-colored and 25 percent colorless ears, while the variegated seeds of the same parent ear would produce 50 percent self, 25 percent colorless and 25 percent variegated. But here comparison of ratios is not necessary—the mere presence of variegated ears, barring accidental pollination, is evidence of the factorial change from *S* to *V*. From a few variegated and partly variegated seeds from self-pollinated parent ears, all the expected classes of ears—self, colorless, and variegated—have been obtained. Only a single variegated ear, however, has been

produced from the few variegated seeds tested. This ear was self-pollinated and threw only variegated and colorless offspring, just as was expected on the basis of the assumed factorial change. But the same result would necessarily have followed if the variegated ear in question had been produced through the action of a stray grain of pollen carrying *V* on a seed that might otherwise have produced a colorless ear. While the chance is rather small that such a stray grain of pollen might have happened to fertilize one of the very few variegated seeds of the parent ear rather than one of the numerous self-colored seeds, the possibility is not excluded. No adequate evidence, therefore, of a factorial change from *S* to *V* is available. It can merely be said that such a change is strongly suggested. The assumption of factorial change is strengthened by the fact that the variegated ears of this lot are more fully colored than those of any other variegated strain in my collection. The few ears observed have more seeds near self, half self, etc., than other strains and more color on the variegated seeds. Moreover, this tendency has persisted to the second generation.

It is of interest to note the fact that in some lots of self-colored maize, which have arisen by sporophytic mutation from variegated strains, no variegated or partially variegated seeds have ever been observed. In other lots, on the contrary, the tendency is very strong to produce a few variegated seeds on the otherwise self-colored ears. In most of these cultures from one-third to two-thirds of the self-colored ears have a few variegated grains. It seems particularly noteworthy that the only cultures to show this apparent reverse mutation trace back to one or the other of two ears of maize obtained some years ago. Some lines of self-colored maize originating from these same two ears have, on the other hand, never shown a tendency to produce variegated seeds.

From all this it seems likely that, if the sporophytic variation here under consideration is a reversal of the common mutation which goes from *V* to *S*, there are differences between the *S* factor of different strains in respect to the frequency with which it may change to a *V* factor just as there are different sorts of *V* factors, one of which, V_m, mutates more readily than another, V_l. The possibility, however, that the difference may not be inherent in the *S* or *V* factors themselves, but may be due to some interaction of other factors with the *S* or *V* factor in certain strains is not precluded.

Another point of no little interest is the fact that up to the present time no variegated seeds have been found on ears known to be homozygous for self color, *SS*, though they have appeared frequently in re-

lated heterozygous families, in which *S* was simplex and associated with simplex *V* or with a factor for colorless pericarp. This, if found to hold when further results have been obtained, will have a bearing upon the question of whether both of the duplex factors ever mutate at the same time (see EMERSON 1913). It has been shown earlier in this paper that as a rule only one of the duplex factors *VV* mutates, thus giving rise to *SV* rather than *SS*. Owing to the dominance of *S* over *V*, a mutation of *S* to *V* affecting only one of the duplex factors in homozygous self-colored maize, would not be visible as a somatic variation, for *VS* could not be distinguished from *SS*.

SUGGESTED EXPLANATION OF THE INHERITANCE OF CERTAIN SPOROPHYTIC VARIATIONS AND THE NON-INHERITANCE OF OTHERS

In this and earlier papers, it has been shown that a sporophytic variation from variegation to near self color of the pericarp of maize is definitely inherited, while quite as striking a variation from light and medium variegation to dark-crown variegation of the pericarp is never inherited. The contrast is particularly noteworthy because the non-inherited dark-crown variegation is apparently always associated with a change in cob color from variegation to self pattern, this change also being non-inherited, while the inherited near self variation of the seed is accompanied by only a slight change in cob color, though the self-colored ears produced by such seeds always have self-colored cobs.

When the difference in behavior was first recognized, it seemed possible that it might be related in some way to the stages in ontogeny at which the sporophytic variations in question arise. It was assumed that the modification to self color takes place previous to the differentiation of the megaspore mother cell and in the direct line of its cell ancestry. On the other hand, the fact that much color develops only near the crown of the seeds of the non-inherited dark-crown variation suggested that this modification might occur late in the development of the pericarp and, therefore, in a line of cell generations collateral to that from which the germ cell arises, rather than in direct line with it. A notable difficulty with any such hypothesis is that a factorial change occurring late in the development of the pericarp could hardly be supposed to influence the color of the underlying cob so that every dark-crown seed would be associated with a self-colored cob spot. Moreover, to account for large patches of near self seeds, it had to be assumed that the factor change might sometimes take place almost simultaneously in the rudiments of every grain so that the grains become self-colored

while the cob remains variegated (EMERSON 1914). The universal appearance of self-colored cobs with self-colored seeds in the progeny of these near self seeds led naturally to subsidiary hypotheses concerning the simultaneous modification of factors for cob and pericarp color (EMERSON 1913).

If further investigation confirms the indications already at hand, all these facts can be harmonized and explained on a simple histological basis, which will render at least some of the hypotheses unnecessary and unwarranted. Microscopic sections of mature seeds made for me by Mr. E. W. LINDSTROM, graduate student in genetics at CORNELL UNIVERSITY, indicate plainly that the outer epidermal layer of cells of the pericarp of near self seeds is without color while the underlying part of the pericarp, except at the crown of the seeds, is largely, if not wholly colored. In contrast to this condition, the dark-crown seeds certainly have color in the outer epidermis of the pericarp and, except at the crown, lack color in much of the underlying part of the pericarp. The sections also show indisputably that there is some deep-lying color even at the sides of these dark-crown grains, but whether this color is confined to epidermal cells has not been determined. According to TRUE (1893), the integuments of the ovule, which are mostly two cells thick and therefore probably mostly epidermal, largely disintegrate as the seed develops, but the thick-walled cells of the inner epidermis of the pericarp remain intact. There is also a possibility that the epidermis of the nucellus may have contributed slightly to the color observed in sections of dark-crown seeds. Wholly self-colored seeds of plants produced from the near self variation apparently have color in both the epidermal and the sub-epidermal cells of the pericarp.

Sections of very young maize ears furnished me by Mr. E. G. ANDERSON, graduate student in genetics at CORNELL UNIVERSITY, show the glumes to have only two layers of cells, except near the base where they are several cells in thickness. From this I infer that even the mature glumes are largely epidermal in origin. If this be true, the dark-crown variation, in which the color is now suspected of being confined to the epidermal layers, would necessarily be associated with self-colored cob spots, while the near self seeds, with presumably no color in epidermal tissue would be associated with glumes that were non-colored, except at their thick bases. The wholly self-colored seeds produced in the next generation by near self seeds should, of course, have self-colored cobs because here there is color in the epidermis as well as in the sub-epidermal cells.

There yet remain to be explained the light crown spot of near self seeds, the exactly corresponding dark crown spot of dark-crown variegated seeds, and the lack of color differentiation at the crown of seeds of self-colored ears produced by near self seeds. While the matter can be settled definitely only by a study of the developing seeds, there are some reasons for the belief that the crowns of maize seeds are largely epidermal in origin. The exact correspondence in pattern between the colored lines converging at the point of attachment of the silk of dark-crown grains and the light spot of near self seeds has been noted repeatedly. So far as I have observed self-colored seeds occurring individually or in small groups within a large "freak" patch of dark-crown seeds and self-colored cob always lack the light crown spot. Likewise, in a large patch of near self seeds with variegated cob, there sometimes occur small patches of self-colored cob and, so far as observed, the seeds of the small patches are wholly self-colored, lacking the light crown spots.

All of these peculiarities of coloration of seeds and cobs are thus readily harmonized, if it turns out on further study that the color of the dark-crown variation is limited to epidermal tissue and the color of the near self variation to sub-epidermal tissue. And, more important still, no other explanation of the non-inheritance of the one type and the inheritance of the other is needed. Sporophytic changes occurring in epidermal cells can, of course, have no influence upon the germ cells which arise from sub-epidermal tissue. Modifications of genetic factors in epidermal cells are doubtless not fundamentally different from such changes in sub-epidermal cells, but if the inheritance of a variation is to remain the criterion of mutation, mere epidermal variations must be regarded at most as nothing more than potential mutations.

In various papers (EMERSON 1911, 1913, 1914), it has been assumed that factors for colors or color patterns of the pericarp are distinct from similar factors of the cob glumes and that these glume and pericarp factors are closely linked. These assumptions were made to account for such observations as the following. When a race having color in both glumes and pericarp is crossed with one lacking color in these parts, no new combinations of glume and pericarp color are produced. When a race having self-colored cob glumes and colorless pericarp is crossed with one having colored pericarp and colorless or nearly colorless glumes, F_1 has color in both glumes and pericarp, but produces no gametes bearing factors for this combination of colors, so that in F_2 there appear only the parental and F_1 combinations, never colorless glumes with colorless pericarp. It was natural to suppose that also in case of variegated peri-

carp and cob glumes separate factors were concerned, namely, V_p, and V_c. To account for the appearance of self-colored cobs with self-colored seeds in the next generation from near self seeds occurring as somatic variations on otherwise variegated ears, it seemed necessary to assume a simultaneous modification of V_p and V_c to S_p and S_c. And this occurrence it was suggested might be due to the close association of V_p and V_c in the chromosomes.

The histological explanation suggested above, of the inheritance of certain, and the non-inheritance of other, sporophytic variations, if found to be correct, will make it seem more likely that the self color and variegation factors responsible for the color patterns of the pericarp are the identical factors concerned with the same color patterns in the glumes. Attention has already been called by MORGAN *et al.* (1915) to the possibility that I have been dealing with cases of multiple allelomorphs rather than with closely linked factors. In the light of the present study MORGAN'S view seems the more reasonable one.

If the explanation here suggested for the inheritance of certain sporophytic variations in maize and the non-inheritance of others is found to be the true one, it will be of interest to investigate similar situations in other plants. It will be remembered that DE VRIES (1905, pp. 309-328) reported the inheritance of a sporophytic change from variegated to self red flower color in Antirrhinum, while CORRENS (1910) described a similar variation in Mirabilis flowers, that is not inherited. I have previously suggested (EMERSON 1914) that these cases may be similar to the inherited and non-inherited sporophytic variations in maize. At present there is nothing more than this resemblance in behavior to suggest a similar explanation, but it is proposed to investigate the situation in these and other variegated flowers.

RELATION OF VARIEGATION TO UNIT-FACTOR CONSTANCY

If the results here recorded have been correctly interpreted, they have an important bearing upon the question of unit-factor constancy. Self-color arises from variegation and is then inherited as a simple allelomorph to variegation. It follows, therefore, that a unit factor concerned in the development of variegated pericarp is occasionally changed to a factor concerned in the development of self color. Moreover, the same change—or a change that produces the same end result—occurs repeatedly. There is some evidence also that a factor for self color thus produced may, by a reverse mutation, become again a factor for variegation.

The variegation and self-color factors belong to a series of not less than nine or ten multiple allelomorphs which include self red and self orange, white-capped red, basal red, and colorless pericarp, associated with either self red or white cobs, and at least three types of variegated pericarp associated with similarly variegated cobs. The fact that such a series of multiple allelomorphs exists is evidence that a fundamental factor concerned in the development of pericarp and cob colors and color patterns has at one time or another mutated in diverse ways. That these several factors are distinct, not merely with respect to the end results which they help to produce as exhibited in types of coloration of mature ears, but also as regards the relative frequency with which they are now mutating, is obvious to anyone who has worked with ear colors of maize. Only two instances of sporophytic changes from self red to white—or perhaps they were from white to red—have been observed by me. Both of these variations were accompanied by modifications of the fundamental color factor concerned (EMERSON 1914). I have also found two ears with both self red and self orange, or brownish orange, seeds in separate patches. There is some scarcely conclusive evidence that in these cases also factorial modifications were responsible for the somatic variations observed. In no other instances, not involving variegation, have such changes been noted. When it is remembered that large numbers of individuals of these types have been studied in pure strains and in crosses, the rarity of such factorial changes becomes evident.

There is some evidence that a self-color factor, that has arisen by mutation from a variegation factor, may, by a reverse mutation, become a variegation factor. The change is comparatively infrequent, not more than five variegated seeds ever having been found on any one otherwise self-colored ear. But it occurs with considerable regularity, for from one third to two thirds of the ears of some heterozygous or partly heterozygous lots have one or more variegated seeds. In some strains of self-colored maize that have arisen by mutation from variegated strains, no tendency to a reverse mutation has been observed. It seems possible, therefore, that there exist distinct self-color factors which produce identical end results—self color—and which differ in no way except in relative frequency of mutation.

Certainly there exist two, and probably three, distinctly different types of variegated pericarp. The most obvious difference between them is in the amount of red (or brown) color produced. But the fundamental difference is probably only a matter of relative frequency of

factorial change. One type is very light variegated, i. e., has little red (or brown) color—few more or less fully self-colored seeds and few even that are prominently striped with color—because the factor concerned changes to a factor for self color comparatively rarely. Medium variegated types have more self-colored seeds and more seeds with prominent stripes of color because in them the factorial change occurs more frequently. In very dark variegated maize (a type little studied as yet) the same change takes place with still greater frequency.

In all types of variegated pericarp, ears with all or nearly all seeds self-colored or near self are less common than ears with small patches of near self seeds. Ears of the latter sort are less common than those with scattered near self seeds. Near self seeds are less commonly seen than half self and the latter less commonly than seeds with broad self-colored stripes. Most common of all are narrow streaks of color. Practically all seeds of medium variegated ears have numerous streaks of that kind. Even the lightest variegated ears have some seeds so marked. All this, I am inclined to believe—although perhaps there is not sufficient evidence to substantiate it—is because the factorial change occurs with increasing frequency in the later stages of ontogeny. If this is true, the several types of variegated pericarp differ in frequency of factorial change by virtue of the fact that the change begins earlier in some types than in others. On this basis colorless seeds of very light variegated ears might be regarded as the extreme of delayed factorial change, for such seeds produce variegated ears rather than colorless ones in later generations.

According to this interpretation, then, there are, in this somewhat remarkable series of multiple allelomorphs, many degrees of factorial constancy. On the one extreme are self-colored and colorless races, both as constant probably as most Mendelian characters. Next to these are the self-colored types that exhibit from one to four or five variegated or partially variegated seeds on perhaps a majority of the heterozygous ears. Then comes the very light variegated type in which a factorial change to self color comparatively rarely occurs at a sufficiently early stage in ontogeny to affect the germ cells but somewhat more frequently at later stages. At the other extreme is a little known type of very dark variegation in which the factorial change occurs so frequently that all ears, so far as observed, have numerous self-colored or near self seeds. Medium variegated races—probably of more than one type—occupy an intermediate place in the series.

There can be no question that at least the more distinct types of

variegated pericarp are inherited in a simple Mendelian way. They segregate out sharply and apparently without contamination. While the factorial changes described are doubtless non-Mendelian, they are in no sense anti-Mendelian. Genetic modifications are not the concern of Mendelism but of mutation. The essential feature of Mendelism is the segregation of unit factors without their contamination. There is a tendency on the part of some to add as another essential the absolute constancy of unit factors. Doubtless most geneticists who have dealt at first hand with Mendelian phenomena regard unit factors as relatively stable. Few presumably, who have studied pedigree cultures extensively, would hesitate, however, to admit the possibility of an occasional rare mutation. If any unit factor may possibly be modified once, may not others change many times? Much recent work, connecting genetical behavior with the cytological phenomena of reproduction, affords convincing evidence that unit factors are, or have their basis in, material substances. Nothing is better known than that specific, even though closely related, organic compounds differ remarkably in their stability. It seems reasonable, therefore, that specific unit factors might differ widely in constancy. But, whether reasonable or not, they appear in fact so to differ.

Perhaps it is too early to venture further in what may prove to be only fanciful speculation. Whether or not, however, the interpretation here suggested is finally accepted, it will best serve its purpose as a tentative hypothesis if it is boldly followed in whatever way it seems to point. With this as justification, then, it is suggested that some of the divergent results of selection within pure lines, or what pass for pure lines, and in clonal populations may find a rational explanation in accordance with the hypothesis developed in this paper. There seems abundant evidence that selection involving several variable characters within pure lines of the common cereals, for instance, has no effect. On the other hand, unpublished results obtained by WEBBER and MYERS leave little room for doubt that selection is often times effective within tuber-lines of the common potato. It does not seem unreasonable to expect many gradations from organisms, in which on the one hand, particular characters respond somewhat readily to pure-line selection, to organisms with which, on the other hand, it will be impossible to demonstrate any such effect.

In view of the foregoing suggestions and in order that there may be no misunderstanding of my position, it may be well to add that I see no reason for abandoning the pure-line concept which has played so

important a part in the clarification of our ideas of inheritance. While we shall have to recognize that it has limitations, there is little in this study to indicate even a lessening of its importance. Even though factorial modification occurs frequently, it can have little influence upon the trend of evolution, if, as in variegated pericarp of maize, it is merely the same modification occurring again and again, and that modification being subject to occasional reversal. Much less is there anything either in the facts here presented or in the speculations concerning them to justify positive assertions of inconstancy of unit factors when the material employed is of questionable purity or when it has not been subjected to careful factorial analysis.

SUMMARY

Distinct variations in variegated ears of maize are described. Results previously reported have been confirmed with more favorable material and new phases of the problem have been investigated. The seed ears used in the later studies have all been pollinated by colorless strains to avoid difficulties arising from the uncertainty of the purity of the pollen of variegated races. Self-colored, partly self-colored, variously variegated and colorless seeds from variegated parent ears, thus pollinated, have given progenies containing a percentage of self-colored ears roughly proportional to the amount of self color in the seeds planted, the maximum being approximately 50 percent from self-colored and near self seeds and the minimum none from colorless seeds. This has been equally true whether the parent ears have been homozygous or heterozygous for pericarp color. In the latter case, the self-colored ears have always occurred at the expense of variegated ears, never at the expense of colorless ones. Medium variegation has been found to be a simple Mendelian dominant to very light variegation. Self-colored ears appearing in the progeny of F_1 ears of this cross have occurred at the expense of medium variegated ears rather than in the place of very light variegated ones. These facts are held to indicate that a genetical factor for variegation mutates to a factor for self color, that only one of the duplex factors ordinarily so mutates, and that the factor for medium variegation mutates much more frequently than that for very light variegation.

Some evidence has been found to indicate the inheritance of a light type of variegation arising as a sporophytic variation on medium variegated ears, but the matter has not been fully investigated. Sufficient evidence has been obtained to warrant the statement that a sporophytic change in type of variegation, resulting in seeds with strongly colored

crown spots associated with self-colored cob glumes, is not inherited as regards either pericarp or glume color.

In a number of cultures of self-colored maize all descended from two presumably unrelated variegated ears, from one to five wholly or partly variegated seeds per ear have occurred on about two thirds of the otherwise fully self-colored ears. Other related and unrelated cultures have not exhibited such exceptional seeds. No variegated seed has, so far as known, ever occurred on a homozygous self-colored ear. A single test has indicated the inheritance of these presumably reverse mutations from self color to variegation, but the question requires further study.

A preliminary histological examination of the developing maize ovary and glumes and of the mature seed has suggested a possible explanation for the peculiarities of coloration of distinct somatic variations and for the inheritance of some of them and non-inheritance of others. The change from variegated to near self seeds associated with little change in color of the glumes is thought to occur only in sub-epidermal cells and for this reason to stand a chance of being inherited, while the change from variegated to dark-crown variegated seeds accompanied by self-colored glumes is believed to be limited to the epidermal layers and hence to be incapable of inheritance.

It is thought that these results favor the idea that single allelomorphic factors, rather than two or more closely linked factors, are responsible for the color pattern of both glumes and pericarp.

The phenomena studied are held to have an important bearing on the question of unit-factor constancy. The existence of the series of at least nine or ten multiple allelomorphs to which variegation belongs, indicates that a factor for pericarp color has mutated several times. Some of the factors of this series have not been observed to mutate, while others have mutated rarely and still others many times. In fact, the principal difference between certain of the factors is thought to lie in their relative frequencies of mutation. It is suggested that data such as is here presented may help to explain the somewhat diverse results of selection experiments within pure lines, clonal lines, and the like.

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THE CORRELATION BETWEEN BODY PIGMENTATION AND EGG PRODUCTION IN THE DOMESTIC FOWL

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INTRODUCTORY REMARKS

Many poultry breeders have criteria by which they feel able to distinguish the laying from the non-laying birds in their flocks at any time without recourse to trap-nesting.[1]

It is perhaps not surprising that with the introduction into agricultural investigations of the exact methods of laboratory experimentation these indirect and scientifically untested criteria should receive but little credence or attention.

Nevertheless it must be admitted that in extended and deep-rooted popular belief there is frequently a minimum of substance as well as a maximum of superstition. We therefore decided to test various popular beliefs against the facts of actual controlled experiments, with a view to

[1] KENT (1916) has recently outlined the criteria employed.

eliminating the mass of superstition and differentiating the kernel of truth if existent.

Such a course seemed to have a two-fold justification.

First, it is perhaps self evident that for many practical breeders trap-nesting is an unattainable ideal. Any method which makes possible the selection of the heaviest layers without the expense of trap-nesting should—providing selection itself is worth while—be of practical value.

Second, egg production in the domestic fowl is a remarkable example of the chemical efficiency of an organism. During the year the 150-egg bird stores in her eggs an amount of fatty and nitrogenous substances which in comparison with her body weight is relatively enormous. It would be highly remarkable if these processes could be carried on without affecting, and perhaps profoundly, the visible somatic features of the organism. If this be true, a study of the correlation between the extent of reproductive activity and somatic characters may have its value from the purely physiological side.

Early in these studies two of us (BLAKESLEE and WARNER, 1915 a, b, BLAKESLEE 1915, WARNER 1916) showed that in certain breeds of poultry, such as Leghorns and the so-called American breeds, including Plymouth Rocks, Wyandottes and Rhode Island Reds, there is in fact a close connection between the amount of yellow pigment to be seen in a bird and her previous laying activity.

Since these observations were published, various comments, criticisms, notes of earlier fragmentary observations, and preliminary notes on work in progress elsewhere have appeared, chiefly in the poultry journals. We shall not, we hope, be considered unfair to other writers if in the present technical treatment of the subject we omit all reference to discussions unaccompanied by quantitative data.

It is our purpose in this place to analyze more minutely, by means of the modern biometric formulae, the data upon which the former conclusions were based and other supplementary series.

In doing this we shall not attempt a comprehensive investigation of all the problems presented by the series of data at our disposal, but shall limit ourselves as strictly as possible to one specific problem, that of the relationship between body pigmentation and egg production. In doing this we are also restricting ourselves to one measure only of pigmentation—the percentage of yellow occurring in the ear lobe of White Leghorns as determined by the color top. This measure is selected because it is probably the most accurate of those available and the most suitable for quantitative expression.

It is, therefore, best fitted for a purely physiological study. The results obtained with this character are substantiated by the results of observations on pigmentation of leg, beak and vent, which will be discussed in detail in a forthcoming bulletin of the STORRS AGRICULTURAL EXPERIMENT STATION.

MEASUREMENTS TAKEN

The amount of yellow in the ear lobe can be conveniently measured quantitatively by means of the Milton Bradley color top. In matching ear lobes against the blend produced by the spinning disk, only yellow and white sectors were used. The matching is not perfect, especially in the lower grades, since a certain amount of blue is often present. The amount of yellow has, however, probably been more accurately measured than if the other color components had been considered. Under proper illumination, it appears possible for an observer to repeat observations with a divergence of not over 5 percent.[2] In analyzing the results statistically, we have recorded in classes of 5 percent range.

Pigmentation determinations were made October 19-21, 1914 and October 17-18, 1915.

The egg records were taken as a part of the regular routine of the egg laying contest. Such details as are essential concerning this feature of the work will be given below.

ACCURACY OF DATA AND SOURCES OF ERROR

Our data were drawn exclusively from the egg laying competitions conducted for the past four years at Storrs, Conn. The method of procedure in these competitions has been described elsewhere (KIRKPATRICK and CARD 1915).

Pullets enter the competition November 1 and remain for one year. They are housed in pens of 10 birds each, are fed the same ration, and so far as possible are treated exactly alike.[3] The influence of environmental factors can therefore be disregarded.

[2] Tests in the use of the top indicate that some observers have a constant tendency to read higher or lower than others, but that an individual observer tends to estimate consistently. Accordingly, all the color determinations upon which constants are based were taken by the same observer (BLAKESLEE).

[3] In 1913-'14 four pens, and in 1914-'15 one pen, belonging to the EXPERIMENT STATION, had sour milk substituted for certain ingredients in the normal ration, but since they showed no apparent difference in color that could be attributed to the change in the feed, they are included in the tabulations.

That the use of such data for physiological studies will be criticized by some we have little doubt. Such criticisms will fall into three principal categories:

1. That the birds entered in these competitions constitute a relatively heterogeneous group of organisms.

The fact that these birds were submitted by a large and widely scattered series of breeders may not, we think, be considered altogether, if at all, a disadvantage. The variety of origin of the birds makes certain that the results are typical of the breeds as a whole, not characteristic of and determined by some peculiarities of a particular experiment station flock.

A certain disadvantage of the materials may possibly lie in the fact that while all the birds were in their pullet year when placed in the competition the exact hatching date of the different lots and the number of eggs which may have been laid by the individuals before they were placed in competition on November 1 is unknown.

The absence of these data is far less important (if of any significance at all) in the kind of problem with which we are dealing in this paper, than they would be in studies involving the records of the total egg production of the first and second year.

2. That the records of egg laying competitions lack the accuracy demanded by scientific investigation.

This we doubt. Relatively large economic importance attaches to the results of these competitions, and every reasonable precaution has been taken to secure trustworthy results.

3. Finally, the objection may be made that the pigmentation determinations by means of the color top could not be carried out with the degree of accuracy necessary for quantitative work.

This objection is not supported by the results of our experience of the past two years, which has shown that it is possible to repeat determinations with a fair degree of consistency, and that experimental errors in matching colors are not great enough to materially influence results when the experiments are carried out on a large scale.

Any objections on these grounds would be equally pertinent to any physiological studies in which the same technique was necessary. The extent of the experiment presents certain great advantages as compared with the usual experimental studies. The number of birds involved was relatively very large. As a result, errors of observation, if not of a systematic nature, will tend to average out.

The smoothness of our results and the remarkable agreement of the

constants for the two years seems to us the strongest *a posteriori* reason to consider the technical details of the work—both those of the egg laying competition, properly so called, and the measurements of pigmentation—as having been carried out with a relatively high degree of consistency and exactness.

PRESENTATION OF DATA AND BIOMETRIC CONSTANTS

As explained above, we shall in this paper limit ourselves as strictly as possible to a consideration of the problem of the relationship between ear lobe pigmentation and egg production. For this purpose it is necessary to know the frequency distribution and the physical variation constants of the characters dealt with.

Type and variation of characters

The frequency of the different percentages of pigmentation in the two years are shown in tables 5 and 6 below, and graphically on a percentage basis in diagrams 1 and 2.

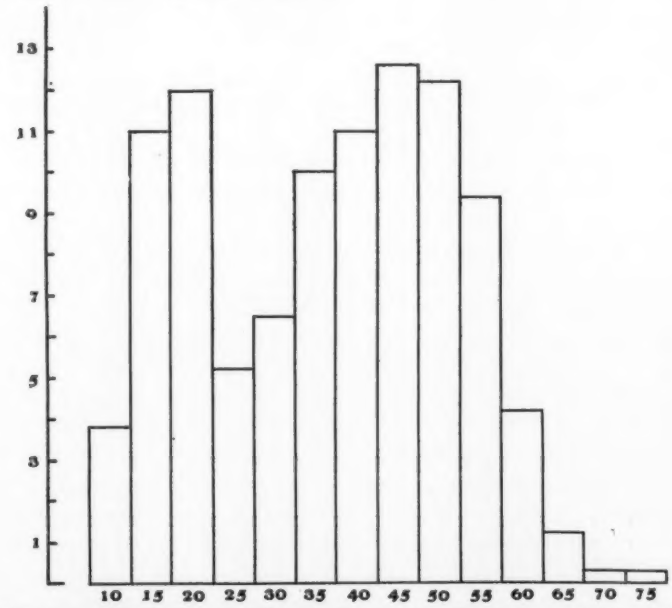


DIAGRAM 1.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1913-'14. Frequencies are reduced to percentages.

These show a highly interesting bimodal condition. The frequency of birds with given percentages of yellow increases from the lowest recorded class, 10 percent, up to 20 percent, beyond which there is a decline in the number of birds observed which reaches its lowest point at 25 or 30 percent. The frequency then rises to a maximum at 45 or 50 percent, after which it again falls. The variation constants in terms of individual percents are as follows:

	Mean	Standard deviation	Coefficient of variation
1913-'14	36.408 ± .579	15.090 ± .409	41.45 ± 1.30
1914-'15	40.640 ± .560	16.079 ± .396	39.56 ± 1.12
Difference	4.232 ± .805	.989 ± .569	1.89 ± 1.72

The difference in the percentage of yellow in the two years is about 5 times as large as its probable error. Such a difference, considered

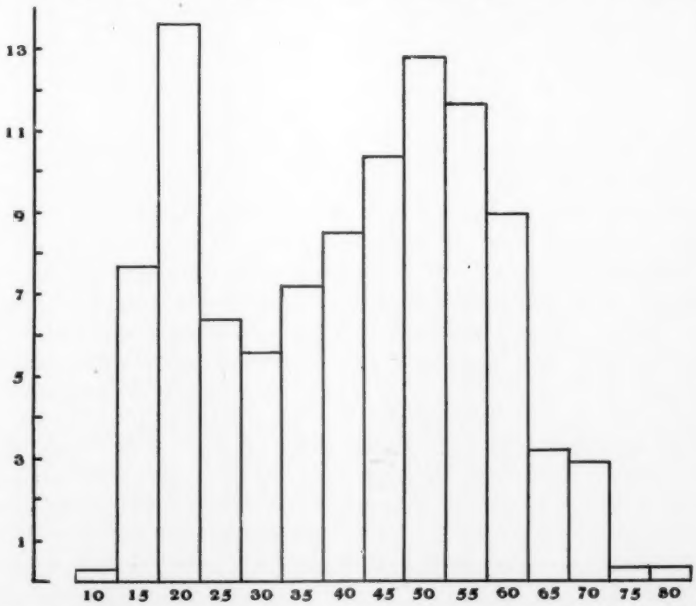


DIAGRAM 2.—Distribution of yellow in five percent classes in ear lobes of White Leghorn hens, 1914-'15. Frequencies are reduced to percentages.

from the purely statistical side, would be looked upon as probably significant. The difference is, however, less than one working unit. When the great difficulties in matching color series under the best conditions are borne in mind, it is not surprising that a difference at least as great as that shown here should be found between the results of two sets of observations separated by an interval of a year.

The variation in the percentage of yellow pigment, measured in the absolute terms of standard deviation or in the relative terms of the coefficient of variation, cannot be said to differ significantly in the two years, when probable errors are taken into consideration.

The variation in number of eggs laid per year is very wide, ranging from 16 to 255 in 1913-'14, and from 0 to 255 in 1914-'15. We give merely the means and variation constants for annual production. These are:

	Mean	Standard deviation	Coefficient of variation
1913-'14	151.63 ± 1.45	37.85 ± 1.03	24.96 ± 0.72
1914-'15	154.48 ± 1.51	43.22 ± 1.06	27.98 ± 0.74
Difference	2.85 ± 2.09	5.37 ± 1.47	3.02 ± 1.03

The mean annual production differs by less than three eggs, or by less than two percent. The birds in the competition in 1914-'15 were perhaps significantly more variable in annual egg production than those studied in 1913-'14.

Notwithstanding the fact that certain differences between the constants for pigmentation and for annual egg production in the two years must be considered statistically significant, the impression which any impartial observer must gain from these constants is that the experiment has been carried out in the two different years with a surprisingly high degree of consistency of results.

For number of eggs laid per month the range is narrow enough that the frequency of birds laying from 0 to 29 eggs, the maximum observed number, may be given for each month individually. Table 1 gives the results for 1913-'14. Table 2 presents those for 1914-'15.

The average number of eggs laid per month by all birds irrespective of their somatic characters are given for the two years in table 3.

TABLE 1

Distribution of birds according to number of eggs laid per month in 1913-1914.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	126	157	158	21	—	—	—	2	4	9	88	184	749
1	26	9	23	12	—	1	—	2	—	5	26	14	118
2	9	5	6	12	—	1	1	—	2	4	14	10	64
3	21	7	16	12	1	—	—	—	1	4	6	4	72
4	13	3	15	3	2	—	1	1	3	—	6	6	53
5	9	9	10	11	1	—	—	1	2	5	4	4	56
6	13	14	9	21	4	1	—	2	1	3	6	3	77
7	10	9	14	19	1	—	—	2	3	3	8	2	71
8	12	14	5	18	1	—	—	2	2	2	6	7	69
9	9	5	15	24	3	2	—	2	3	4	3	8	78
10	10	7	8	17	2	3	—	4	10	8	4	5	78
11	9	7	5	22	7	4	4	8	8	9	5	8	96
12	12	7	4	16	7	6	3	8	6	4	5	2	80
13	6	5	5	17	14	4	2	6	5	6	6	5	81
14	4	5	7	17	17	8	5	8	9	6	5	3	94
15	10	7	1	22	16	8	3	7	5	8	7	3	97
16	7	6	3	15	26	17	5	7	10	16	11	5	128
17	1	6	2	17	25	15	9	7	11	9	12	10	124
18	1	5	2	8	33	22	15	17	13	17	16	9	158
19	—	7	1	3	32	32	16	19	17	11	18	5	161
20	1	7	—	1	40	47	22	27	27	30	19	8	229
21	—	—	—	1	26	44	27	32	21	24	17	2	194
22	—	5	—	—	27	43	48	31	35	32	11	2	234
23	—	3	—	—	15	31	50	47	38	36	3	—	223
24	—	—	—	—	7	16	41	25	31	36	2	—	158
25	—	—	—	—	1	3	24	24	13	9	1	—	75
26	—	—	—	—	1	1	18	10	21	7	—	—	58
27	—	—	—	—	—	—	10	6	6	1	—	—	23
28	—	—	—	—	—	—	5	2	1	—	—	—	8
29	—	—	—	—	—	—	—	—	1	1	—	—	2
Totals	309	309	309	309	309	309	309	309	309	309	309	309	3708

The differences show how closely the results of the two competitions agreed in their results for mean egg production month by month. Absolutely the differences are small, but relatively they are rather large in comparison with the average egg production of either of the two years, which is of course itself low in the winter months.

It does not seem worth while in this place to consider the magnitudes of these differences in comparison with that of the absolute values upon which they are based or to offer any theories concerning the causes of the observed discrepancies.

That the differences are statistically trustworthy may be seen from the fact that they are often several times as large as their probable errors, as is shown by the final column, in which the ratios have been obtained

TABLE 2

Distribution of birds according to number of eggs laid per month in 1914-1915.

Eggs laid	November	December	January	February	March	April	May	June	July	August	September	October	Annual total
0	152	103	133	47	8	4	3	11	12	25	69	190	757
1	20	14	12	18	1	1	2	2	5	9	16	23	123
2	10	12	16	16	1	—	—	—	1	5	6	14	81
3	16	17	22	15	2	1	1	4	6	3	3	12	102
4	13	13	13	19	2	1	1	—	2	4	5	12	85
5	7	18	15	24	5	4	2	3	2	9	5	13	107
6	18	23	11	21	5	—	1	6	2	1	3	10	101
7	9	17	14	18	8	3	3	4	2	4	4	7	93
8	14	13	15	30	10	2	6	—	3	4	2	8	107
9	14	10	10	18	3	5	8	4	6	8	5	7	98
10	15	15	14	21	13	9	3	5	5	1	6	7	114
11	12	16	11	12	14	7	3	5	5	5	10	4	104
12	18	8	16	20	8	5	2	7	9	7	6	6	112
13	10	11	12	12	16	10	7	7	7	8	12	6	118
14	7	7	8	17	21	25	9	4	9	11	11	7	136
15	13	16	8	21	27	19	6	5	9	8	17	7	156
16	6	12	5	14	23	26	10	4	6	10	20	8	144
17	3	17	14	12	22	30	7	4	11	17	23	8	168
18	4	9	8	12	29	32	13	12	16	24	24	7	190
19	5	12	8	2	39	43	25	12	17	14	25	7	200
20	1	5	6	5	42	39	22	17	22	29	29	6	223
21	6	5	3	1	33	40	45	45	23	36	32	4	273
22	—	1	1	—	15	23	39	41	41	50	16	1	228
23	1	—	—	—	18	25	50	50	36	40	13	1	234
24	—	1	—	—	8	13	42	53	39	25	6	—	187
25	1	—	—	—	1	5	29	33	41	10	6	—	126
26	—	—	—	—	1	2	23	23	25	5	—	—	79
27	—	—	—	—	—	1	10	11	10	3	—	—	35
28	—	—	—	—	—	—	2	2	2	—	1	—	7
29	—	—	—	—	—	—	1	1	1	—	—	—	3
Totals	375	375	375	375	375	375	375	375	375	375	375	375	4500

by dividing the differences by their probable errors.[4] Thus the performance of the birds at any stated time differed significantly in the two years. Just such differences should be expected. It is perhaps rather surprising that they are not larger. The birds are entirely different series of individuals. The conditions under which the birds were maintained prior to their installation in the contest probably differed somewhat. Finally, while conditions in the two years of the contest are intended to be as nearly as possible the same, it is quite clear that homologous months in two successive winters will rarely be identical in climatic conditions.

[4] Probable errors have been calculated by the conventional formulae, notwithstanding the abnormal nature of the frequency distributions.

TABLE 3

Mean number of eggs, and probable error of mean number of eggs, laid by all birds for each month.

Month	Mean eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	4.282 ± .197	5.368 ± .214	+1.086 ± .291	3.73
December	5.217 ± .262	7.219 ± .231	+2.002 ± .349	5.74
January	3.294 ± .178	6.056 ± .223	+2.762 ± .285	9.69
February	9.456 ± .204	8.104 ± .198	−1.352 ± .284	4.76
March	17.702 ± .155	16.125 ± .188	−1.577 ± .244	6.46
April	19.405 ± .140	17.701 ± .162	−1.704 ± .214	7.96
May	21.712 ± .141	20.339 ± .187	−1.373 ± .234	5.87
June	19.874 ± .198	20.080 ± .223	+ .206 ± .298	.69
July	19.379 ± .224	19.267 ± .239	− .112 ± .327	.34
August	17.919 ± .259	16.848 ± .263	−1.071 ± .369	2.90
September	9.133 ± .330	12.904 ± .291	+3.771 ± .440	8.57
October	4.262 ± .256	4.467 ± .223	+ .205 ± .339	.60

Table 4 gives the variation constants for number of eggs laid per month. Comparisons between the results of the two years may again be made by means of the difference column. Many of the differences are several times as large as their probable errors. Thus the variation in

TABLE 4

Standard deviations and probable errors of standard deviations of number of eggs laid per month by all birds.

Month	Standard deviation of eggs laid			
	1913-1914	1914-1915	Difference	Diff./E. Diff.
November	5.134 ± .139	6.140 ± .151	+1.006 ± .205	4.91
December	6.822 ± .185	6.644 ± .164	− .178 ± .247	.72
January	4.639 ± .126	6.408 ± .158	+1.769 ± .201	8.80
February	5.316 ± .144	5.687 ± .140	+ .371 ± .201	1.85
March	4.028 ± .109	5.399 ± .133	+1.371 ± .172	7.97
April	3.640 ± .099	4.660 ± .115	+1.020 ± .152	6.71
May	3.671 ± .100	5.360 ± .132	+1.689 ± .166	10.17
June	5.151 ± .140	6.392 ± .157	+1.241 ± .210	5.91
July	5.847 ± .159	6.874 ± .169	+1.027 ± .232	4.43
August	6.751 ± .183	7.556 ± .186	+ .805 ± .261	3.08
September	8.597 ± .233	8.365 ± .206	− .232 ± .311	.75
October	6.678 ± .181	6.397 ± .158	− .281 ± .240	1.17

egg production in the individual months must be considered to differ significantly in the two experiments. Such differences should be expected for the reasons set forth in the discussion of the means above. The question of the differences between the variabilities at comparable times in the two years or at various times in the same year requires no more detailed discussion here, where the chief value of the standard deviations is to furnish one step towards the correlation coefficients.

Correlation of pigmentation and egg production

Table 5 for 1913-'14 and table 6 for 1914-'15 give the frequency with which birds of different pigmentation classes occur in the two years and the total number of eggs laid by birds of these classes in each month and for the entire year of the two contests. From these totals the mean

TABLE 5

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1913-1914.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	12	75	108	64	140	234	257	278	247	275	265	224	202	2369
15	34	215	279	176	378	606	665	747	710	746	749	622	456	6349
20	37	220	304	172	402	707	710	848	818	811	759	624	426	6801
25	16	70	68	55	130	261	312	357	345	317	342	262	129	2648
30	20	56	105	86	203	340	342	422	379	390	377	205	64	2969
35	31	94	150	94	329	536	592	638	588	557	548	171	14	4311
40	34	127	134	90	295	591	680	725	634	673	593	219	5	4766
45	39	134	175	72	300	702	766	852	801	730	658	202	9	5401
50	38	132	135	83	327	653	726	808	713	679	597	150	9	5012
55	29	129	120	82	262	521	565	643	572	546	463	107	2	4012
60	13	71	34	44	119	213	264	273	218	203	151	31	—	1621
65	4	—	—	—	35	72	79	83	75	58	35	5	1	443
70	1	—	—	—	—	15	19	12	21	3	—	—	—	70
75	1	—	—	—	2	19	19	23	20	—	—	—	—	83

egg production of birds of a given class may be computed for any period, or data for the determination of the correlation between pigmentation and egg production may be deduced (HARRIS 1910).

Consider first the correlation for October pigmentation and egg production for the entire year.

The nature of the relationship between the concentration of yellow pigment in the ear lobe and the annual egg record of the bird may be most clearly exhibited to the statistically untrained reader by means of

TABLE 6

Frequency of birds showing various percentages of yellow and total number of eggs laid by them in each month and during the whole year 1914-1915.

Percent yellow	Number of birds	Total eggs												Annual total
		November	December	January	February	March	April	May	June	July	August	September	October	
10	1	11	·20	3	20	20	19	25	24	22	18	23	10	215
15	29	186	284	241	278	483	551	619	614	622	542	591	409	5420
20	51	332	461	384	449	837	930	1141	1124	1087	1021	975	616	9357
25	24	136	228	192	225	401	417	511	539	515	464	447	270	4345
30	21	116	184	183	168	365	363	452	450	466	420	365	114	3646
35	27	165	203	219	261	469	467	525	534	529	487	428	122	4409
40	32	196	179	158	255	476	525	644	591	564	549	452	48	4637
45	39	182	280	195	317	648	745	798	832	792	728	554	44	6115
50	48	289	296	271	388	769	836	940	919	932	793	455	25	6913
55	44	199	267	193	293	655	748	864	794	682	634	360	4	5703
60	34	118	155	100	237	514	586	629	677	620	395	94	2	4127
65	12	44	70	62	67	188	208	231	226	237	192	67	1	1593
70	11	35	68	70	66	184	199	206	185	157	75	28	—	1273
75	1	—	5	—	8	18	22	19	—	—	—	—	—	72
80	1	4	7	—	7	20	22	23	21	—	—	—	—	104

TABLE 7

Mean number of eggs per year laid by birds showing different percentages of yellow in the two years. The number of birds upon which the averages are based is also shown.

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10	12	197.4	1	215.0
15	34	186.7	29	186.9
20	37	183.8	51	183.5
25	16	165.5	24	181.0
30	20	148.5	21	173.6
35	31	139.1	27	163.3
40	34	140.2	32	144.9
45	39	138.5	39	156.8
50	38	131.9	48	144.0
55	29	138.3	44	129.6
60	13	124.7	34	121.4
65	4	110.8	12	132.8
70	1	70.0	11	115.7
75	1	83.0	1	72.0
80	—	——	1	104.0

the averages of the annual egg production of birds of different pigmentation grades. The results are given in table 7.

The average number of eggs laid per year decreases rapidly from about 200 in birds with 10 percent of yellow to less than 150 in those with over 40-45 percent of yellow in the ear lobes.

The great practical value of the relationship as a means of selecting the best birds may be best seen by grouping these records.

The results are shown in table 7A. Here the birds with 10, 15 and

TABLE 7 A

Percent yellow	1913-1914		1914-1915	
	Birds	Mean eggs	Birds	Mean eggs
10—20	83	187.0	81	185.1
25—35	67	148.2	72	172.2
40—50	111	136.7	119	148.4
55—65	46	132.1	90	126.9
70—80	2	76.5	13	111.5

20 percent yellow are clubbed together, those with 25, 30 and 35 percent form a second group, and so on.

Neglecting the few birds recorded as possessing an unusually high percentage of yellow, i.e., 70-80 percent, it is clear that there are differences of the highest practical significance in the birds constituting the four groups which are sufficiently large to give trustworthy averages. By selecting in October for breeding purposes birds with 10-20 percent yellow, the poultryman will secure a group which have averaged over 30 eggs above the flock as a whole and over 50 eggs above the average of the class with 55-65 percent of yellow. It is to be noted that these differences are not merely very great indeed, but that the group of high-laying birds (10-20 percent yellow) is sufficiently large for economic purposes. Surely eighty birds out of every three or four hundred ought to be a sufficiently liberal number in practical selection operations.

The results may now be expressed in terms of correlation. Summing the products of the total annual egg production, E, by the grades of percentage of yellow, y, for the individual birds, we have

$$\text{For 1913-'14, } \Sigma\,(yE) = 1{,}603{,}225$$
$$\text{For 1914-'15, } \Sigma\,(yE) = 2{,}216{,}875$$

whence by the formula used (HARRIS 1910),

$$r_{yE} = \frac{\Sigma\,(yE)/N = \bar{y}\bar{E}}{\sigma_y\ \sigma_E}$$

where the bars denote the means and the sigmas the standard deviations as given above, we find numerically[5]

For 1913-'14, $N = 309$

$$r = \frac{\Sigma\,(yE)/N - 36.407769 \times 151.134306}{15.090082 \times 37.853644} = -.5816$$

For 1914-'15, $N = 375$

$$r = \frac{\Sigma\,(yE)/N - 40.640000 \times 154.477335}{16.078673 \times 43.222447} = -.5271$$

Thus the relationship between the October ear lobe pigmentation as measured in units of 5 percent range and the annual egg production of the domestic fowl is surprisingly high.

The differences for the two years in the intensity of the relationship is

For 1913-'14, r_{yE} =	$-.5816 \pm .0253$
For 1914-'15, r_{yE} =	$-.5271 \pm .0252$
Difference	$.0545 \pm .0358$

The difference is only about fifty percent larger than its probable error, and cannot be considered statistically significant. Conversely, the results for the two years may be considered practically identical.

The correlation coefficients show on the uniform standard scale of -1 to $+1$ the degree of interdependence of two variables, in this case the percentage of yellow in the ear lobe and the egg record of the domestic fowl. For many purposes measures on such a standard scale are of the highest value. For other comparisons it is desirable to determine not merely the relationship between percentage yellow and egg production on a *relative* scale but also to know just how much birds with different percentages of yellow differ in terms of actual mean number of eggs laid. Such absolute measures have the disadvantage that they are not comparable with measures of the same or other characters taken on the same or any other organism at any other place or time. Thus the two methods supplement each other. Fortunately it is possible to pass at once from relative measures in terms of correlation to absolute values in terms of regression.

[5] In the calculations involved in this paper all the operations have, of course, been carried to a larger number of places than are given in the tables.

The conventional formula, in terms of the present notation, is

$$E = (\bar{E} - r\frac{\sigma_E}{\sigma_y})\bar{y} + r\frac{\sigma_E}{\sigma_y}y$$

where E = eggs laid, y = percent yellow, the bars denote the mean values of the characters and the sigmas their standard deviations in the population as a whole.

The actual equations are

For 1913-'14, $E = 204.754 - 1.459\ y$
For 1914-'15, $E = 212.058 - 1.416\ y$

The second term of the equation shows the *decrease* in annual mean number of eggs laid for each *increase* of one percent of yellow in the ear lobe. Since determinations of yellow are recorded in units of 5 percent range, the second term may be multiplied by five to obtain the actual difference in egg production associated with a difference of one working unit in pigmentation. This will be noted to be about 7 eggs in both years.

These absolute changes may be represented graphically by the slope of a straight line. The points at which such a line cuts the ordinates erected upon the various percentages of yellow, mark off the theoretical mean number of eggs laid by birds of this grade of pigmentation. By theoretical mean number is to be understood merely the mean number which has been calculated from the trend of the data as a whole, on the assumption that the rate of change may be satisfactorily represented by the slope of a straight line. How satisfactorily it can be thus represented is most conveniently determined by a comparison of the theoretical, or smoothed, and the empirical means calculated directly from the data available for the particular class alone.

Such lines are shown for the two years in diagram 3. The actual means from table 7 above are also represented. The agreement of the empirical and theoretical means is not as good as might be wished, but it does not seem desirable on the basis of the present data to consider in any greater detail the precise form of the theoretical line which would best smooth these empirical averages.

Turn now to the interrelationship for the individual months.

The correlations between the percentages of yellow observed in October and egg production for the individual months are given for the two years in table 8.

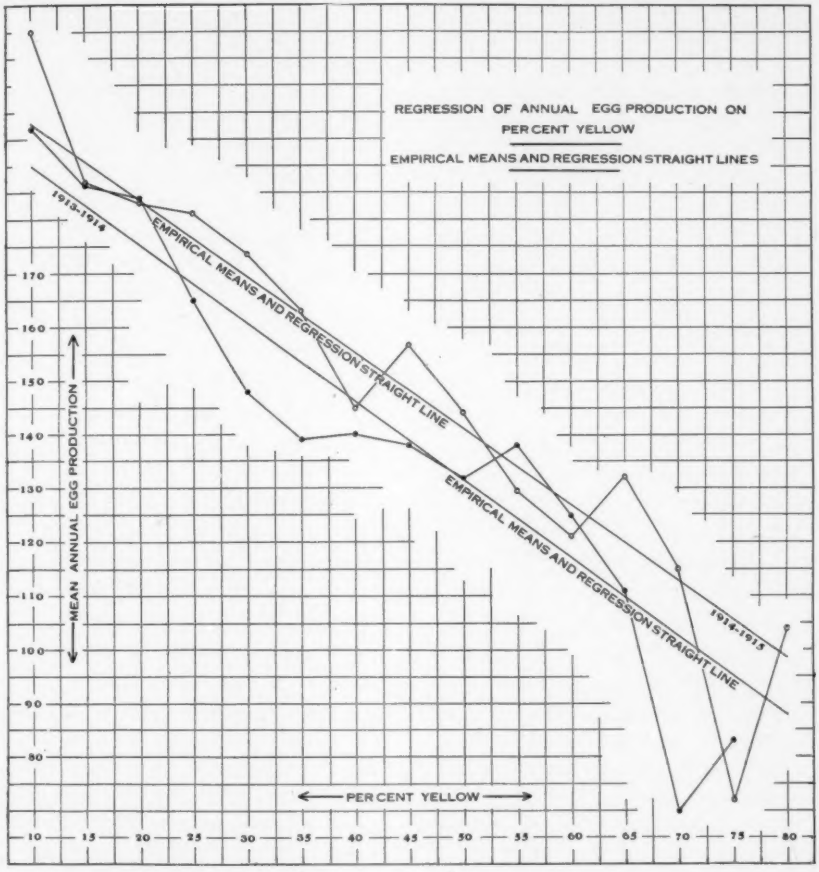


DIAGRAM 3.—Relationship between percent yellow in ear lobes in October and annual egg production. The closed and open circles show the observed mean numbers of eggs laid by birds with varying percentages of yellow. The straight lines represent the equations for the regression of egg production on percent of yellow. They show, on the same ordinates as the empirical averages, the smoothed (theoretical) means calculated from the data as a whole.

Before discussing the absolute magnitudes or the statistical significance of the constants for the individual months, we may draw attention to the consistency of the results for the two years. First of all, it is clear at a glance that although many of the coefficients are low, they are

TABLE 8

Correlations and probable errors of correlations between percent yellow in ear lobes in October and egg production for the individual months of the years, 1913-1914, 1914-1915, and their differences.

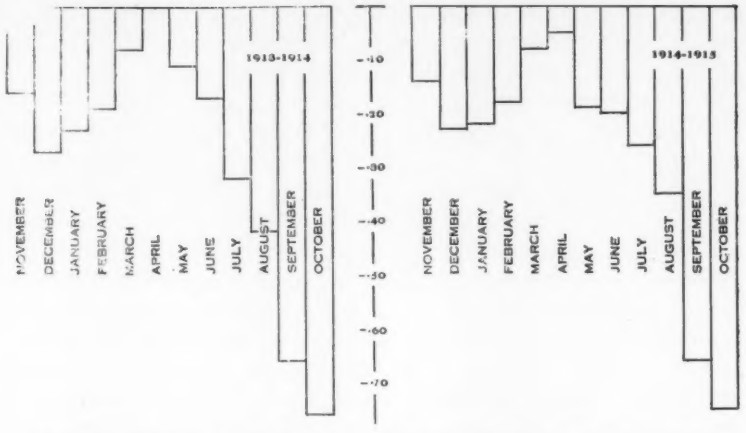
Month	Correlation 1913-1914	r/Er	Correlation 1914-1915	r/Er	Difference in correlation 1913-1914, 1914-1915	Diff./E. Diff.
November	—.167 ± .037	4.51	—.148 ± .027	5.48	—.019 ± .046	0.41
December	—.271 ± .036	7.53	—.230 ± .033	6.97	—.041 ± .049	0.84
January	—.229 ± .036	6.36	—.228 ± .033	6.91	—.001 ± .049	0.02
February	—.193 ± .037	5.22	—.176 ± .034	5.18	—.017 ± .050	0.34
March	—.086 ± .038	2.26	—.080 ± .035	2.29	—.006 ± .052	0.12
April	—.000 ± .038	0.00	—.056 ± .035	1.60	+.056 ± .052	1.08
May	—.114 ± .038	3.00	—.194 ± .034	5.71	+.080 ± .051	1.57
June	—.170 ± .037	4.60	—.202 ± .033	6.12	+.032 ± .050	0.64
July	—.324 ± .034	9.53	—.267 ± .032	8.34	—.057 ± .047	1.21
August	—.429 ± .031	13.84	—.354 ± .030	11.80	—.075 ± .044	1.70
September	—.663 ± .022	30.14	—.663 ± .020	33.15	+.000 ± .030	0.00
October	—.761 ± .016	47.56	—.751 ± .015	50.07	—.010 ± .022	0.45

negative throughout. Comparison of the results for the individual months is facilitated by the column giving the differences and their probable errors. In 8 cases the correlation for 1913-'14 is numerically larger than that for 1914-'15, in 3 cases it is smaller and in one month the coefficients are identical for the first three figures. The absolute magnitude of the differences is of relatively little importance if they are not statistically significant. By dividing these absolute differences by their probable errors, as has been done to obtain the values in the final column of the table, comparable measures of the significance of the differences are obtained. By common consent among statisticians a difference should be at least 2 or 2.5 times as large as its probable error to be regarded as significant—i.e. to be considered to be due to some other cause than the errors of random sampling merely. Of the ratios in this final column not a single one indicates a difference between the coefficients of the two years as much as twice its probable error, only 4 out of the 12 ratios are larger than unity, and the average value is only 0.70. In the discussion of the correlation *for the entire year* it has been shown that the coefficients are, *within the limits of the errors of random sampling,* identical. The results just given show that *in not a single instance can the correlations for the same individual months in the two years be considered to differ significantly.*

We must confess that this result is a matter of some surprise, as well as of gratification to ourselves. Knowing the difficulties of the work and realizing the possible sources of error we were quite prepared to find coefficients distributed with great irregularity and differing by many times their probable errors in the two series of observations. Instead we find results of a higher degree of consistency than are often secured in cases in which theoretically the most refined measurements may be made. A stronger proof of the general accuracy and trustworthiness of our work could not, we believe, be adduced.

As a further means of comparison of the results of the two years, and as a first introduction to the subject of the magnitude of the coefficients for the individual months, diagrams 4 and 5 have been prepared. The two graphs show that the coefficients for the same month in the two years are sensibly identical. They also show that the correlations differ widely from period to period, increasing from the earlier to the later months of the test.

The rate of increase from the first to the last month of the experiment is not, however, uniform. The correlation increases in numerical magnitude from November to December, then it diminishes until it is



DIAGRAMS 4 and 5.—Magnitude of correlation between October ear lobe pigmentation and egg production in the individual months of the two competitions. Distance which the bars extend below the zero line indicates the magnitude of the negative correlations.

practically non-existent in April, after which time it rises rapidly to its maximum value in October. Were there but a single series of data one might suspect the bimodal distribution observed, to be due to chance, but the remarkable agreement of the results for the two years at once throws out this possibility. Furthermore the relation of the constants to their probable errors is such as to leave little doubt concerning the reality of the bimodal nature of the distribution which as a whole shows pronounced skewness. With the exception of the months of March and April only, the constants are three or more times as large as their probable errors. Thus only in April may the correlations be said to be sensibly zero.

Before discussing in detail this question of the differences between the correlations for the various months of the year it seems better to express the results in terms of regression.

The equations appear in table 9. Since yellow is measured in units of five percent range, the amount of change to be expected for a deviation of one working unit has been added in the column headed "change per unit of yellow."

The empirical means for the individual months are calculated from the frequencies and total egg productions recorded in tables 5 and 6. The results are shown for the first three months, November, December

TABLE 9

Straight line equations showing the regression of number of eggs laid per month upon October ear lobe pigmentation.

Month	1913-1914		1914-1915	
	Regression equation	Change per unit* of yellow	Regression equation	Change per unit* of yellow
November	$E = 6.355 - .057\ y$	.29	$E = 7.664 - .057\ y$	.29
December	$E = 9.677 - .122\ y$	.61	$E = 11.083 - .095\ y$	.48
January	$E = 5.860 - .070\ y$	.35	$E = 9.755 - .091\ y$	.46
February	$E = 11.937 - .068\ y$	.34	$E = 10.628 - .062\ y$	.31
March	$E = 18.543 - .023\ y$	.12	$E = 17.219 - .027\ y$	.14
April	$E = 19.405 - .000\ y$	.00	$E = 18.359 - .016\ y$	.08
May	$E = 22.723 - .028\ y$	.14	$E = 22.965 - .065\ y$	.33
June	$E = 21.987 - .058\ y$	.29	$E = 23.343 - .080\ y$	.40
July	$E = 23.942 - .125\ y$	.63	$E = 23.902 - .114\ y$	.57
August	$E = 24.907 - .192\ y$	.96	$E = 23.605 - .166\ y$	.83
September	$E = 22.890 - .378\ y$	1.89	$E = 26.923 - .345\ y$	1.73
October	$E = 16.527 - .337\ y$	1.69	$E = 16.612 - .299\ y$	1.50

* Unit = 5 percent.

and January, in diagram 6, for the months February, March and April in diagram 7, for the months May, June and July in diagram 8, for August in diagram 9, for September in diagram 10, and for October in diagram 11.

In these graphs the varying slope of the lines indicates the amount of change in egg production associated with variations of the amount indicated in the percentage of pigment. Since all are drawn to the same scale direct comparisons between them are possible. It is clear, for example, that the rate of change decreases from the first winter months of the experiment to April, when the line shows practically no slope and that it again increases until, in the late summer and early autumn months of August, September and October, the slope of the lines is very steep indeed. All this may be seen from the tables. The diagrams further show—and this is their greatest value—that for all the months excepting October, a straight line furnishes as good a graduation as could be expected from any curve of a higher order. To be sure there is great irregularity in the distribution of the empirical means about the theoretical means given by the straight line, but such discrepancy is regularly and necessarily found as a result of random sampling when

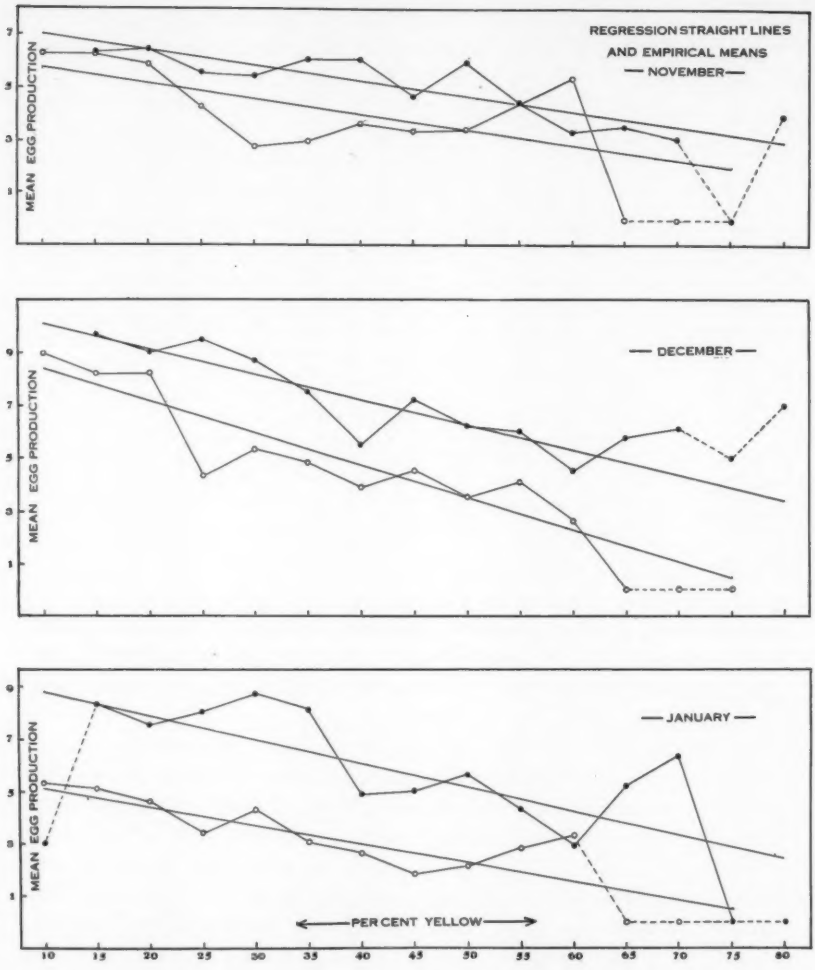

REGRESSION STRAIGHT LINES
AND EMPIRICAL MEANS
— NOVEMBER —
MEAN EGG PRODUCTION
— DECEMBER —
MEAN EGG PRODUCTION
— JANUARY —
MEAN EGG PRODUCTION
PERCENT YELLOW
10 15 20 25 30 35 40 45 50 55 60 65 70 75 80

DIAGRAM 6.—Regression of egg production on percent yellow in ear lobes in October for the individual months November, December and January. Compare explanation of diagram 3.

the number of observations is not large and correlation is of a low order of magnitude.

To the exception to the rule of a sensibly linear relationship between

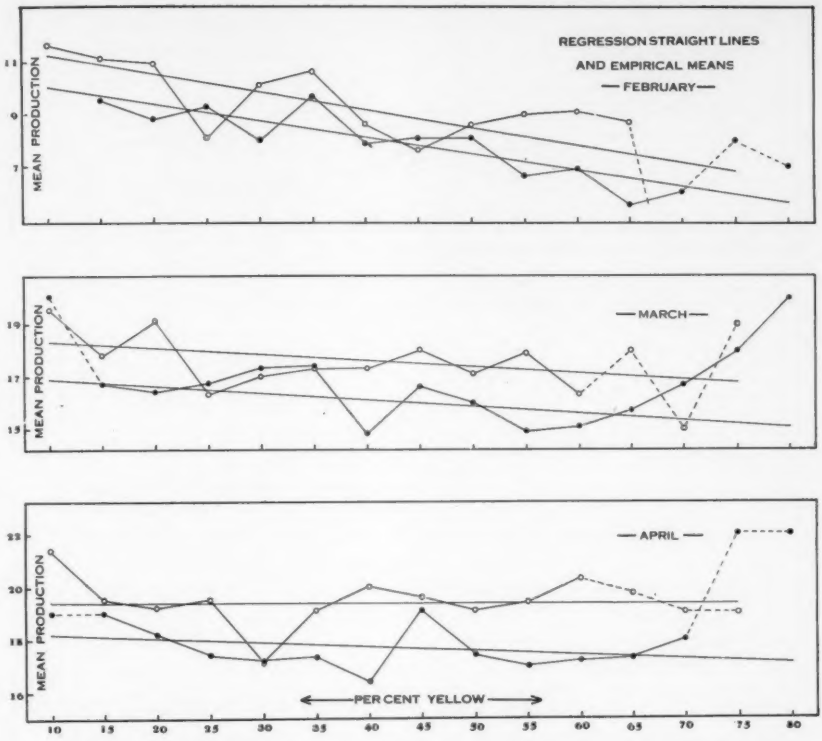


DIAGRAM 7.—Regression of egg production on percent yellow in ear lobes in October for the individual months February, March and April.

percentage of yellow and egg record we shall return in a subsequent section.

The maximum rates of change are found in the winter and autumn months. Thus in December there is a decrease of about half an egg for each increase of 5 percent in October pigmentation. In August, September and October the change is much greater. In March, April and May it is at a minimum.

ATTEMPTED ANALYSIS OF OBSERVED INTERRELATIONSHIPS

In this section we shall attempt by the means of further analysis to interpret certain of the relationships established in the foregoing pages.

One of the most suggestive peculiarities of the measures of inter-

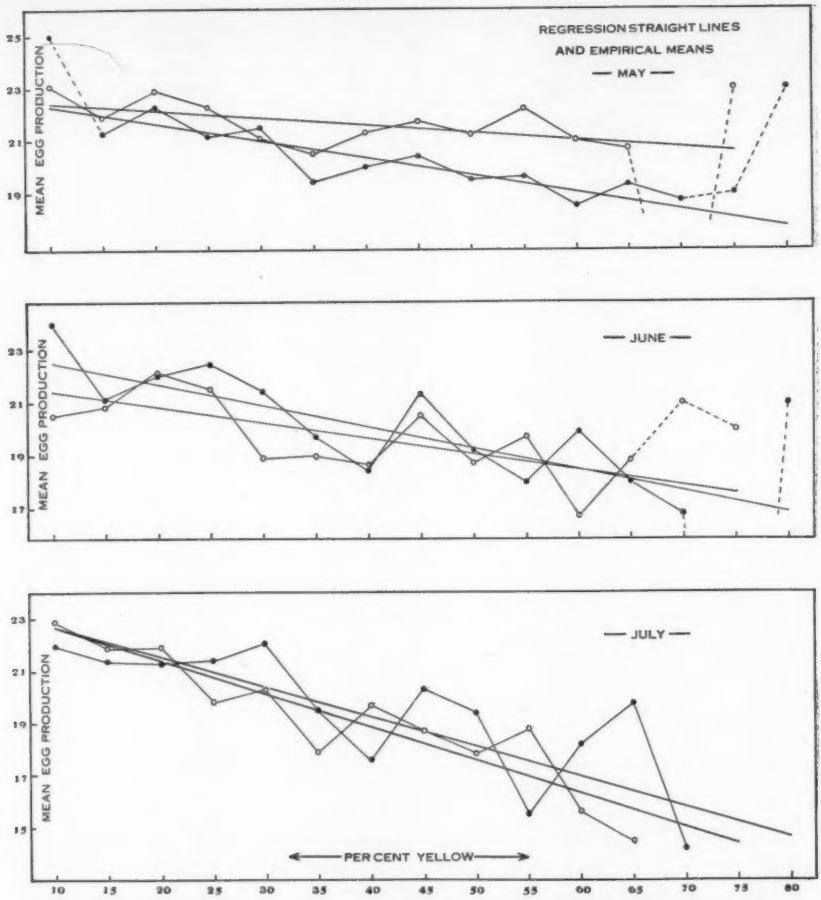

REGRESSION STRAIGHT LINES
AND EMPIRICAL MEANS
— MAY —
— JUNE —
— JULY —
MEAN EGG PRODUCTION
PER CENT YELLOW
10 15 20 25 30 35 40 45 50 55 60 65 70 75 80

DIAGRAM 8.—Regression of egg production on percent yellow in ear lobes in October for the individual months May, June and July.

dependence of pigmentation and egg production is the difference in the intensity of this relationship exhibited by the several months of the year. If the relationship between pigmentation and egg production be a purely physiological one, at least in some of its essentials, one might expect that the highest correlations would be those determined when the two variables are closely associated in time. This has been shown to be, roughly speaking, the case. It is perfectly clear from the correlations

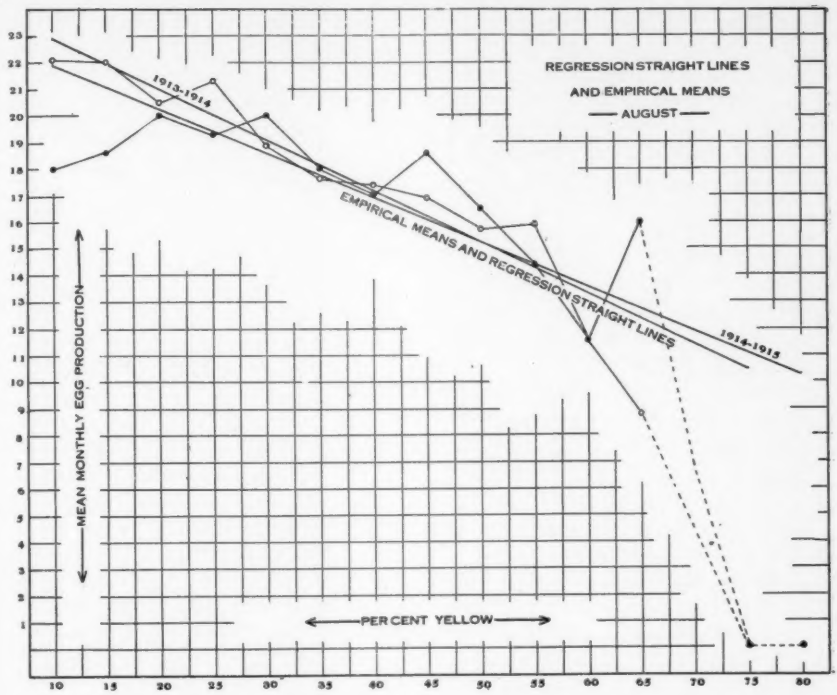


DIAGRAM 9.—Regression of egg production on percent yellow in October for the month of August.

given in table 8, from the regressions shown in table 9, or from the correlations represented in diagrams 4 and 5, or the regressions shown in diagrams 6 to 11, that the numerical magnitude of the interdependence increases toward the end of the experiment. To avoid any possible confusion the reader must always bear in mind that the pigmentation determinations were taken at the end, and (unfortunately) only at the end, of the egg-laying contest.

A priori the most logical hypothesis to account for the relationship observed would seem to be that the growth of the egg abstracts certain substances—in the present case the pigment—from the body tissues with a resulting negative correlation between egg production and quantity of pigment present. This would at once account for the generally

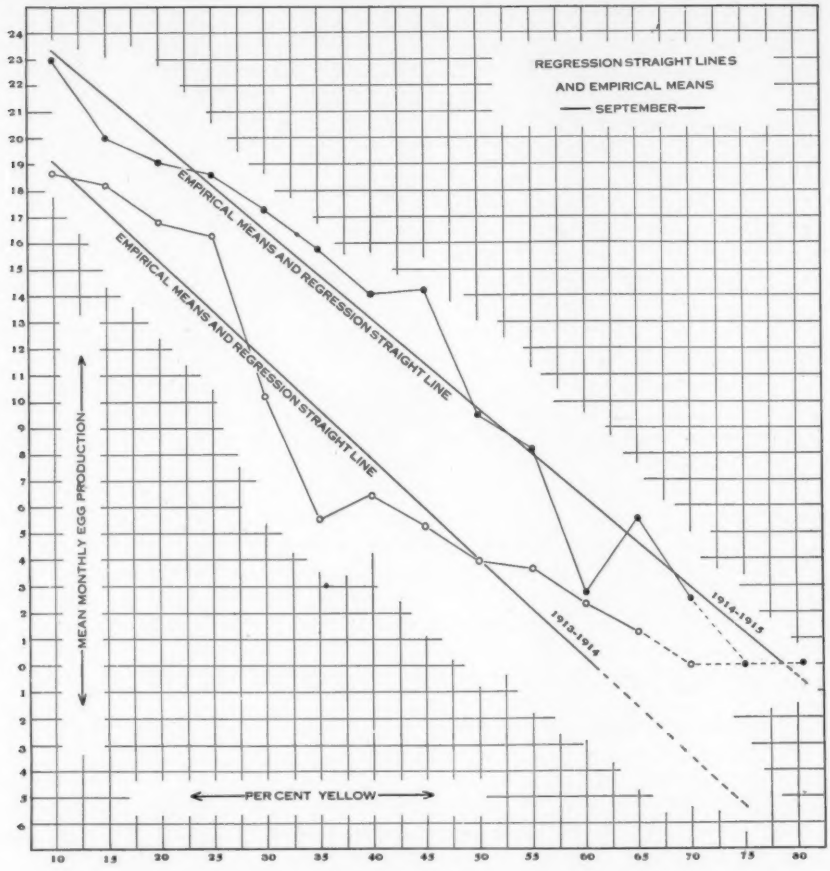


DIAGRAM 10.—Regression of egg production on percent yellow in October for the month of September.

higher correlation between measures made at more closely associated periods of time. If this hypothesis be true, one would expect the maximum correlation to come in or near whatever month the pigment determinations were made.

If this view be the correct one, the (relatively) independent variable would be egg production, the dependent variable would be pigmentation. Egg production would then be looked upon, provisionally at least, as the

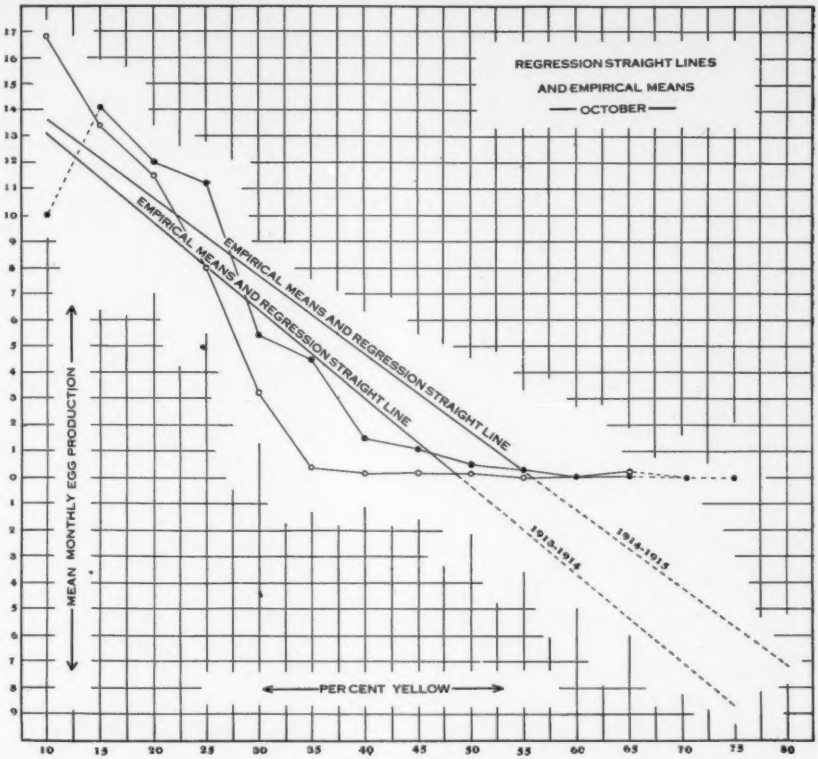

REGRESSION STRAIGHT LINES
AND EMPIRICAL MEANS
— OCTOBER —
EMPIRICAL MEANS AND REGRESSION STRAIGHT LINE
EMPIRICAL MEANS AND REGRESSION STRAIGHT LINE
1913-1914
1914-1915
MEAN MONTHLY EGG PRODUCTION
PER CENT YELLOW
10 15 20 25 30 35 40 45 50 55 60 65 70 75 80

DIAGRAM 11.—Regression of egg production in October on the percent yellow in the ear lobes in the same month.

(chief) proximate cause of the observed intensity of pigmentation. Heretofore in this paper pigmentation has apparently been taken as the more fundamental character. This was not because we believed it to be so *physiologically*, but because we have been seeking to determine the prediction value of a somatic character for use in the selection of birds with a high egg record without actually determining that record by trap-nesting.

Bearing these considerations in mind it is most instructive to compare the distribution of yellow among the birds with different egg records when the egg records are taken in the same month as the pigmentation

TABLE 10

Percent yellow in October 1914 and egg production in November 1913.

November, 1913, egg production	October, 1914, pigmentation														
	10	15	20	25	30	35	40	45	50	55	60	65	70	75	Totals
0	3	12	8	4	9	17	14	17	21	13	2	4	1	1	126
1		2	7	2	3	1	3	2	3	1	2				26
2	3	1		1		2			2						9
3			2	3	3	3	4	3	2		1				21
4			1				2	6	1	1	2				13
5			2	1			1	1		2	2				9
6		2	1	2	1	1	2	1		1	2				13
7		1	1			3	1	2		2					10
8		3	2		1			2	2	2					12
9	1	1			2		3			2					9
10		2	4	1				2		1					10
11	1	2				1	1	1	1	2					9
12	3	2	2	1	1	1	1	1							12
13	1		3						1	1					6
14			1			1	1		1						4
15		3	2					1	3	1					10
16		3				1	1		1		1				7
17			1												1
18				1											1
19															0
20											1				1
Totals	12	34	37	16	20	31	34	39	38	29	13	4	1	1	309

determinations and when the two determinations are separated by a wide interval of time.

The tables for November egg production and October pigmentation represent the most widely separated records. Those for October egg production and October pigmentation represent the most closely associated measurements of the two characters. These two months are, furthermore, particularly suited to our present purposes because in each case a very high and fairly similar percentage of the birds laid no eggs at all. The percentages of birds which laid no eggs are:

	November	October
1913-'14	40.78	59.87
1914-'15	40.53	50.67

For the remaining fecundity classes, the range of variation and the distribution of the frequencies as shown by the total columns are very similar.

TABLE II

Percent yellow in October 1914 and egg production in October 1914.

October egg production	October pigmentation														
	10	15	20	25	30	35	40	45	50	55	60	65	70	75	Totals
0			2	3	10	25	32	34	33	28	13	3	1	1	185
1			1	2		2	1	3	3			1			13
2		1	1		3	2		1	1	1					10
3			1		1	1			1						4
4		1	1	1	1		1	1							6
5		1	2			1									4
6			2		1										3
7			1	1											2
8		2	2	1	2										7
9		3	4	1											8
10	1	2	1	1											5
11		4	2	2											8
12		1	1												2
13	2	1		1	1										5
14		3													3
15	1		2												3
16		2	1	1	1										5
17	2	3	5												10
18	2	5	1	1											9
19	2	2	1												5
20		3	4	1											8
21	1		1												2
22	1		1												2
Totals	12	34	37	16	20	31	34	39	38	29	13	4	1	1	309

The distribution of the birds in the bodies of tables 10 and 11 for 1913 and of tables 12 and 13 for 1914-'15, is however very different. In the case of the November production for each year the birds of all the different fecundities are scattered with a fair degree of uniformity over the whole range of pigmentation. In October, however, the birds which have laid no eggs at all show a distribution of yellow pigmentation which is far more heavily represented in the higher classes of yellow than are those which are laying. Furthermore it is quite evident from these tables that in October, pigmentation decreases very rapidly as one passes from birds which have laid no eggs to those which have laid 1, 2, 3 or more eggs, but that this decrease soon falls off so that birds which have laid over about 6 or 7 eggs are apparently sensibly alike in the amount of yellow which they exhibit.

The same point may of course be shown by computing the average percent yellow for birds of each class with respect to egg production. These are shown in diagrams 12 and 13.

TABLE 12

Percent yellow in October 1915 and egg production in November 1914.

November, 1914, egg production	October, 1915, pigmentation															
	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	Totals
0		10	16	8	6	11	12	17	19	20	21	7	4	1		152
1			1	2	3		2	2	3	2	1	1	3			20
2		1	1	1	2			1	1	1	1		1			10
3		1	3	2	1	2	2	3	1		1					16
4			2		1	1	1	1	1	3		1	1		1	13
5			3			1		1		1	1					7
6		2	2	2	1		3	1	2	4	1					18
7			3			2	1		1	1	1					9
8		2	3	2		1		3	1	2						14
9		2	2			1	2	2	4	1						14
10		4	2	1	1			1	2	2	2					15
11	1	2	1	1			1	1	3		1	1				12
12		1	2		2	3	2	1	3	3			1			18
13		1	4	1	1					1	1	1				10
14						2	1	1	1		1		1			7
15		2	1	1	1	2		2	1	1	1	1				13
16			1	2	1		1		1							6
17				1			1	1								3
18		1			1		1	1								4
19			1						2	2						5
20							1									1
21			2				1		2		1					6
22																0
23			1													1
24																0
25						1										1
Totals	1	29	51	24	21	27	32	39	48	44	34	12	11	1	1	375

The straight lines in these diagrams are calculated from the equations:

For November, 1913, $y = 38.514 - 0.492\ e$
For October, 1914, $y = 43.740 - 1.720\ e$
For November, 1914, $y = 42.720 - 0.388\ e$
For October, 1915, $y = 49.073 - 1.888\ e$

The minus quantities in these equations show that *if the rate of change in pigmentation were uniform from the lowest to the highest layers,* which it is not in October, the yellow decreases less than half a percent for each additional egg laid by a bird in November, but about one and three quarters percent for each egg laid in October.

It is quite clear that in the case of the November egg records the percent yellow changes but slowly and irregularly with egg production,

TABLE 13

Percent yellow in October 1915 and egg production in October 1915.

October pigmentation

October egg production	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	Totals
0			3	2	5	10	19	22	35	37	33	11	11	1	1	190
1					2		4	8	5	3		1				23
2			1			1	2	1	6	2	1					14
3			1			4	1	4	1	1						12
4		1	1	2	2	4		1		1						12
5		1	3		4	2	1	1	1							13
6			3	1	1	1	3	1								10
7			1		3		2	1								7
8		5	1	2												8
9		1	2	3		1										7
10	1	1	3	1	1											7
11			3	1												4
12		1	2	2	1											6
13		2	3	1												6
14		3	2	2												7
15		3	2	1		1										7
16			4	2	1	1										8
17		1	5	1		1										8
18		2	5													7
19		3	2		1	1										7
20		1	4	1												6
21		3		1												4
22				1												1
23		1														1
Totals	1	29	51	24	21	27	32	39	48	44	34	12	11	1	1	375

whereas in the October series the yellow pigment falls very rapidly at first, but thereafter remains practically uniform up to the highest egg classes.

The biological inference to be drawn from this result would seem to be that the egg production of a recent period influences very profoundly the concentration of yellow pigment, so that there is a very rapid decrease in yellow pigment for each additional egg laid, up to a certain point, beyond which the body pigment is relatively little reduced by extra egg production. Thus for October the change in pigmentation is to be described by a curve, not by the slope of a straight line. The change in pigmentation is not proportional to egg production, but at first is very rapid and then falls off.

The point has been investigated in a somewhat different manner in our preliminary paper (BLAKESLEE and WARNER 1915 a, b). There a table is given showing the distribution of 932 records made on 317

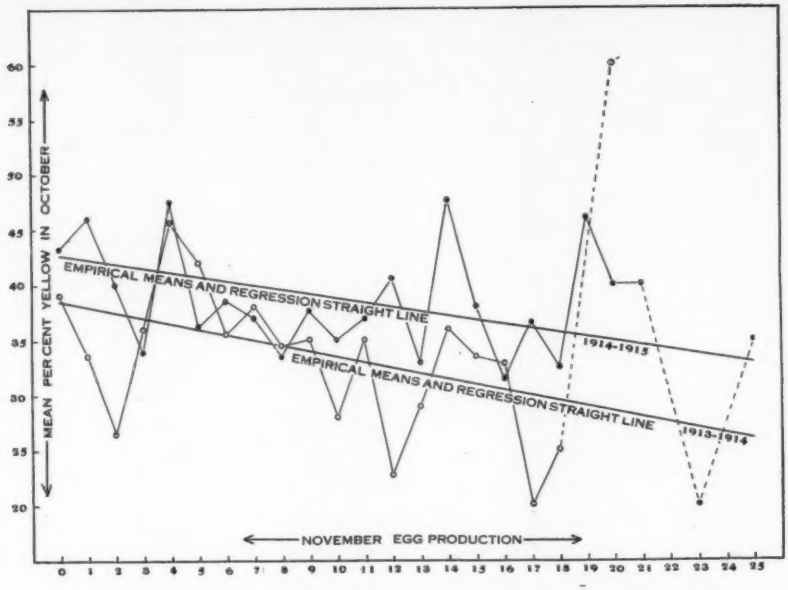


DIAGRAM 12.—Regression of percent of yellow in ear lobes in October on egg production of the *preceding* November. The closed and open circles show the mean percentage of yellow in October for birds laying various numbers of eggs in November. Note the very gentle slope of the lines and the great irregularity in the distribution of the empirical means. Compare diagram 13.

White Leghorns in three series of observations in October of the 1913-'14 competition. The records summarized in this table were made to show the length of time since laying for birds of the various pigment grades. In collecting these data a bird which laid on the day the pigment determination was made or on a later day within the month was considered to be laying, and was recorded in the zero class, i.e., no days since laying. If she laid on the day before the record was taken but not later she is recorded as one day since laying, and so on.

In the table, the results of which are represented graphically in diagram 14, the data are treated in two ways. First of all, the percentage of the birds of various pigmentation classes which are "laying" or "not laying" at the time the color determinations were made, is given. These are represented by the ordinates connected by the light line in the diagram. The percentage of the birds which are laying falls precipitously

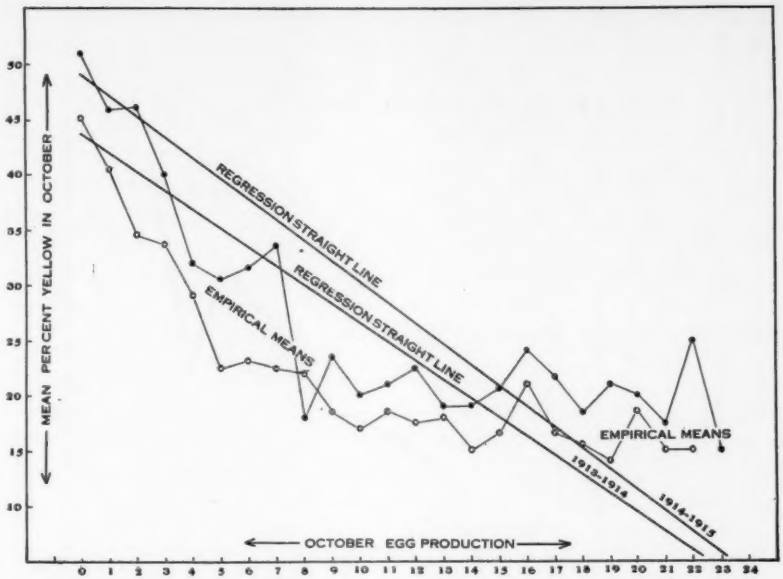


DIAGRAM 13.—Regression of percent of yellow in ear lobes in October on egg production for the same month. Note that as egg production increases the mean percentage of yellow decreases very rapidly, not slowly as in the case of the regression of October pigmentation on the egg production of the preceding November as shown in diagram 12. Note also that the change in percent of yellow is not a uniform one, as is approximately true in the case of the relationship shown in diagram 12, but that the rate of decrease falls off as the heavier-laying classes of birds are reached.

from 87.8 percent among those showing only 6-10 percent yellow, to practically zero for all grades of yellow above 30 percent.[6]

The average number of days since laying has also been computed. This is shown by the heavy line in the diagram. Beginning with an average of only .4 day since laying, in the 6-10 percent color class, the average length of time since laying increases rapidly. Probably the irregularity just before the upper limit of 71 days is due to the small number of records.

[6] The three cases of laying, among 557 records, in the grades above 30 percent yellow were for sporadic layers. The one in the 40 percent group laid October 18, but at no other time in October or September. This case may perhaps be an error in the egg record. One of the two in the 50 percent grade laid during October only on the 2nd, 4th and 25th, though she laid 18 eggs in September; the other laid during October only on the 16th and 19th and had no eggs to her credit in the second half of September.

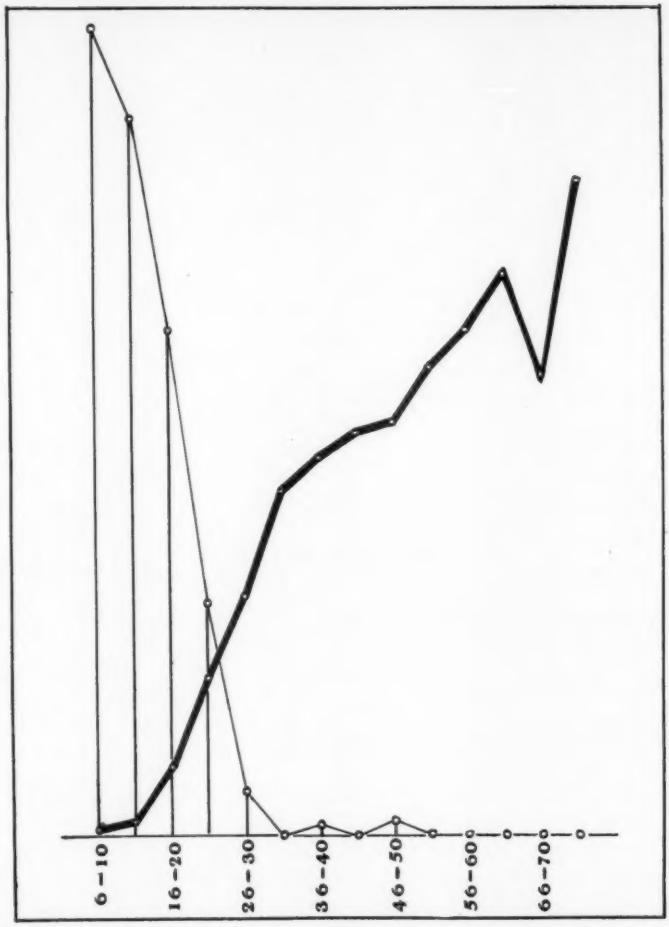


DIAGRAM 14.—Percentage of birds which are laying (light line) and mean number of days since laying (heavy line) in birds with different grades of ear lobe pigmentation.

We now turn to a different aspect of the problem.

If the relationship between percentage of yellow and egg production be chiefly of a physiological nature, it is quite conceivable that the correlations between the October percentage of yellow and egg production during the earlier months of the experiment, may be largely the resultant of other interrelationships. Let us consider this possibility in detail.

Yellow pigment is closely correlated with October egg production. Inspection of the values of the correlation coefficients for percentage yellow and egg production of the individual months shows that the correlation decreases as the monthly egg record becomes farther distant in time from the date of color determination. The decrease is not a uniform one.

If the October egg production of a bird be correlated with her egg production for each of the preceding months of the experiment, then these two interrelationships would tend to bring about a correlation between October pigmentation and the egg production of every other month in the year.

A quantitative measure of the influence of this factor may be secured as follows:

Let r_{ye_1}, r_{ye_2}, $r_{ye_3} \cdots r_{ye_{12}}$ be the correlations between percent yellow in the twelfth month of the contest and egg production in the first, second, third ... twelfth months respectively. Further let $r_{e_{12}e_1}$ $r_{e_{12}e_2}$, $r_{e_{12}e_3} \cdots r_{e_{12}e_{11}}$ be the correlations between October and November, October and December, October and January ... October and September egg productions. If now the values of r_{ye_1}, r_{ye_2}, r_{ye_3} $\cdots r_{ye_{11}}$ be in large part the resultants of $r_{e_{12}e_1}$ and $r_{ye_{12}}$, $r_{e_{12}e_2}$ and $r_{ye_{12}}$, $r_{e_{12}e_3}$ and $r_{ye_{12}} \cdots r_{e_{12}e_{11}}$ and $r_{ye_{12}}$, material reductions in the values of r_{ye_1}, r_{ye_2}, $r_{ye_3} \cdots r_{ye_{11}}$ should result from the rendering constant of the variable e_{12}. Hence applying the well known partial correlation formula for one variable, e_{12}, constant we have:

$$e_{12}r_{ye_1} = \frac{r_{ye_1} - r_{ye_2}\, r_{e_{12}e_1}}{\sqrt{1 - r_{ye_{12}}^2}\ \sqrt{1 - r_{e_{12}e_1}^2}},$$

$$e_{12}r_{ye_2} = \frac{r_{ye_2} - r_{ye_{12}}\, r_{e_{12}e_2}}{\sqrt{1 - r_{ye_{12}}^2}\ \sqrt{1 - r_{e_{12}e_2}^2}},$$

$$e_{12}r_{ye_3} = \frac{r_{ye_3} - r_{ye_{12}}\, r_{e_{12}e_3}}{\sqrt{1 - r_{ye_{12}}^2}\ \sqrt{1 - r_{e_{12}e_3}^2}},$$

$$\vdots \qquad\qquad \vdots$$

$$e_{12}r_{ye_{11}} = \frac{r_{ye_{11}} - r_{ye_{12}}\, r_{e_{12}e_{11}}}{\sqrt{1 - r_{ye_{12}}^2}\ \sqrt{1 - r_{e_{12}e_{11}}^2}}.$$

The evaluations of these equations require merely the calculation of 24 new correlations, the values of $r_{e_{12}e_1}$, $r_{e_{12}e_2}$, ... $r_{e_{12}e_{11}}$ for the two years. These constants are given in table 14. They are positive throughout, indicating that birds which excelled in egg production in October gave on an average higher productions in every other month of the year. The intensity of the correlations, however, varies greatly from the first to the eleventh month. This point does not, however,

TABLE 14

Correlation between October egg production and the egg production of the other eleven months of the year.

Correlation between October and:	1913-1914	1914-1915	Differences	Diff./E. Diff.
November	.219 ± .037	.139 ± .034	—.080 ± .050	1.60
December	.333 ± .034	.253 ± .033	—.080 ± .047	1.70
January	.255 ± .036	.236 ± .033	—.019 ± .049	.39
February	.219 ± .037	.207 ± .033	—.012 ± .050	.24
March	.139 ± .038	.130 ± .034	—.009 ± .051	.18
April	.043 ± .038	.116 ± .034	+.073 ± .051	1.43
May	.207 ± .037	.217 ± .033	+.010 ± .050	.20
June	.265 ± .036	.170 ± .034	—.095 ± .050	1.90
July	.326 ± .034	.271 ± .032	—.055 ± .047	1.17
August	.365 ± .033	.305 ± .032	—.060 ± .046	1.30
September	.694 ± .020	.579 ± .023	—.115 ± .030	3.83

especially concern us in this place. The results for the two years are very closely similar. In only one case is the difference between the coefficient obtained for the 1913-'14 and the 1914-'15 competition twice as large as its probable error. The results are generally lower in 1914-'15 than in the first of the two competitions.

Inserting these values (kept to a larger number of decimal places) in the above equations, we find the results set forth in table 15.

The results are also represented graphically in diagrams 15 and 16. Here the bars on the negative side of the zero bar indicate by their lengths the magnitude of the (negative) correlation between October pigmentation and egg production for the 12 individual months of the year. In this feature the diagram is merely a repetition of diagrams 4 and 5, above. The shaded areas superimposed upon these are the partial correlation coefficients from table 15.

The magnitudes of the interrelationships have been very greatly reduced by correcting for variable egg production in October. Since the correlation so nearly disappears in the early months when correction is made for October egg record, it seems reasonable to conclude that the correlation between yellow pigment in October and egg production in the earlier months of the year cannot be looked upon as indicating that there are strains of birds characterized by lighter pigmentation that are better layers, and that a mixture of all these strains in the flock results

TABLE 15

Partial correlations and probable errors of October pigmentation and egg production in remaining eleven months for constant October egg production.

Month	Partial correlation and probable error	
	1913-1914	1914-1915
November	—.001 ± .038	—.067 ± .035
December	—.029 ± .038	—.064 ± .035
January	—.056 ± .038	—.079 ± .035
February	—.042 ± .038	—.031 ± .035
March	+.030 ± .038	+.027 ± .035
April	+.051 ± .038	+.048 ± .035
May	+.068 ± .038	—.048 ± .035
June	+.051 ± .038	—.114 ± .034
July	—.123 ± .038	—.099 ± .035
August	—.251 ± .036	—.199 ± .033
September	—.289 ± .035	—.424 ± .029

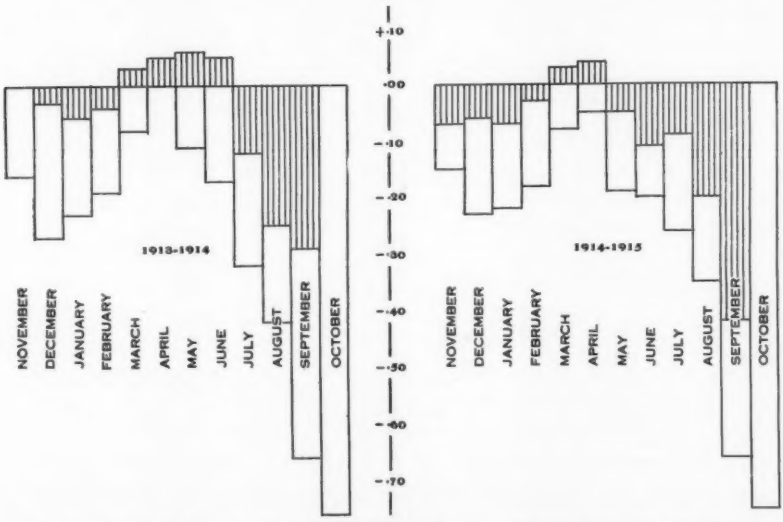
in correlations of the kind which we have demonstrated. The indications are rather that egg production in the earlier months is related to October pigmentation because the birds which are better layers in the early months are also better layers in the fall months, and because October egg production is closely correlated with October pigmentation.

That the correction for October egg production should not so nearly eliminate the correlation between October pigmentation and the egg production of the immediately preceding months, say August and September, is perhaps due to the fact that eggs developed and laid in these months or developed in these months and laid in a subsequent month, must—if the purely physiological theory be the correct one—influence profoundly the pigmentation measured in October.

BIOLOGICAL HYPOTHESES IN EXPLANATION OF THE OBSERVED CORRELATIONS

While the primary purpose of this paper has been the presentation of data and the statistical constants showing the relationship between body pigmentation (ear lobe pigmentation only, in the present paper) and egg production deduced from them, it is proper to refer briefly to the underlying physiological causes of the demonstrated relationships.

The simplest hypothesis is, as pointed out above, that in heavy laying the large quantity of yolk substance produced removes the yellow pig-



DIAGRAMS 15 and 16.—Correlations between October pigmentation and egg production for individual months (unshaded polygon) and partial correlations between October pigmentation and egg production for the individual months (shaded polygon). In the partial correlations, the influence of the correlation of the egg production of November to September with that of October upon the correlation of the egg record for November to September with October pigmentation is eliminated.

ment from the somatic tissue more rapidly than it can be replaced. This is the suggestion offered in an anonymous press letter (1914) from the MAINE AGRICULTURAL EXPERIMENT STATION and by BLAKESLEE and WARNER (1915 a, b).

Since we have been unable to contribute purely chemical data to the problem, it will be sufficient to point out merely that such observations

as have been reported by others from the field of physiological chemistry are quite consistent with the above view.

The nature of the pigment of the ear lobe of the domestic fowl has not been directly demonstrated, but BARROWS (1914) finds that the yellow shank color is due to yellow fat deposits in the Malpighian layers of the epidermis. It seems most reasonable to consider the color of the ear lobe due to an identical fat-soluble pigment.

While concerned primarily with the problem of fat deposition in, and fat absorption from, the egg, RIDDLE (1911, pp. 475-476) in discussing the mechanism of pigment deposition, says:

> "As a concluding word on the rôle of the partition coefficient we record our belief that it alone accounts for the presence of the yolk coloring matter—vitello-lutein and vitello-rubin—in the yellow yolk and not in the white. These are lipochrome pigments, soluble only in fat and fat solvents and are abundant in the large yolk spherules, probably because, as we have shown by comparative analyses, these spherules abound in fat."

Turning now to the more purely chemical literature it is important to note that SCHENCK (*fide* PALMER 1915) as early as 1904 indicated that the pigment of the yolk of the egg and of the blood serum of the hen is identical with one of the forms of xanthophyll,—L-xanthophyll,—which he had isolated from plant tissue. More recent work by WILLSTÄTTER and ESCHER (*fide* PALMER 1915), who have isolated the pigment from the yolks of 6000 hen's eggs, leads them to the conclusion that the principal coloring material of the fowl's egg is isomeric with the crystalline xanthophyll of the chloroplast. PALMER (1915) from his chemical and feeding studies holds that xanthophyll is the principal natural pigment of the egg yolk, body fat and blood serum of the hen, just as he and one of his associates (ECKLES) earlier showed that carotin is the natural pigment in the corpus luteum, body fat, blood serum and milk fat of the cow.

The chief interest of these studies in the present connection is that they indicate *the identity of body and yolk pigment*, thus supporting the view that the correlations here demonstrated rest primarily upon physiological phenomena of the migration of fat-soluble yellow pigment.

The best source of information concerning the mechanism of pigment redistribution is work on feeding of Sudan III and other substances capable of staining fat in the living organism initiated in the investigation of the physiology of the bird by RIDDLE (1907, 1908, 1910, 1911) and continued by GAGE and GAGE (1908), MENDEL and DANIELS (1912), ROGERS (1912) and others. Those who are interested in the details of this subject from the standpoint of the physiological chemist must turn

to the original papers. For the purposes of the present paper it is sufficient to point out that in the later rapidly developing stages of the yolk of the fowl's egg Sudan III will be taken up from the alimentary canal in large quantities. Indeed, RIDDLE has shown that, with heavy feeding, perceptible amounts of the stain will appear in the egg at the end of two or three hours. As the studies of GAGE and GAGE (1908) and others have shown, the Sudan III may be transferred from the yolk fat to that of the young chick.

The generalization to be drawn from the many varied experiments with Sudan III is that while in the animal body it clings at all times to the fats or their constituent fatty acids, and so goes quite mechanically wherever these particles go. This does not, however, preclude the possibilities of differential distribution of the pigment throughout the body. Nor does it preclude the possibility that the fat of the egg may withdraw pigment from the fat of the body tissues.[7] The ovum of the fowl has not merely the capacity of taking up the fat (and with it the Sudan III stain) from recently injected food, but of developing at the expense of body (stored) fat as well.

For the purposes of the present discussion nothing need be said concerning the manner in which either the fat or the fat-soluble pigment which goes along with it, is carried in the blood, or concerning the mechanism of its distribution throughout the body, or of its translocation from body tissues to the yolk. For all such data, which are as yet far from complete, the reader must consult the original physiological literature.

RECAPITULATION

The present paper is a contribution to the general problem of the relationship between somatic characters and fecundity. Specifically it presents and analyzes by means of the modern higher statistics, data bearing upon the relationship between the concentration of yellow pigment in the ear lobe of White Leghorn hens and their egg records of the preceding months.

The data comprise pigmentation evaluations and egg records for 309 and 375 birds entered in the 1913-'14 and 1914-'15 International Egg-Laying Contest held at Storrs, Connecticut.

[7] A quite analogous case of the withdrawal of the pigment from the tissues by the developing egg is furnished by the natural pigment of the egg of salmon. It is practically certain that here the natural coloring matter is derived from the muscles of the fish, from which the fat in which most if not all the coloring matter resides, is transferred to the ovary and to the growing eggs.

The egg records cover a period of one year, November to October, inclusive, of the pullet year. Pigmentation determinations were made in October, that is at the close of the laying period considered. The measures of yellow pigment concentration were obtained by the use of the white and yellow sectors of the color top. The ear lobe was selected for measurement because it presented the least practical difficulty in the quantitative measurement of pigmentation. The results here presented will be confirmed by more qualitative determinations made for these and other birds on the leg, beak and vent.

Incidental to the discussion of the main problem, considerable series of constants for mean fecundity and for variation and correlation in fecundity in the White Leghorn are given. For these the reader must refer to discussions in the body of the paper. With regard to the central problem, the statistical analysis of the data leads to the following conclusions:

There is a very close interdependence between October ear lobe color and the egg production of the year. Numerically the correlation, measured on the universally applicable scale of —1 to +1, is expressed by a constant of the order $r = -.550$. The negative sign indicates that *higher* concentrations of yellow pigment are associated with *lower* annual egg record. The results for the two years are in close agreement.

Expressed in absolute instead of relative terms, the correlations determined indicate that on an average birds differing by 5 percent in the amount of yellow in the ear lobe will differ by about 7 eggs in their annual production. Thus the difference is one of very real practical significance. For example, birds showing only 10-20 percent of yellow in their ear lobes in October will have laid on an average about 185 eggs each, whereas, birds exhibiting 55-65 percent of yellow will have an average annual production of only about 130 eggs.

The correlations between October pigmentation and the egg production of each month of the year have also been determined for the two years. All of these coefficients are negative in sign. Thus they show that a high percentage of yellow in October indicates lower egg production not merely in the year as a whole, but in each individual month of the year as well. Almost without exception these coefficients may be considered significant in comparison with their probable errors. The results for the individual months are in remarkably good agreement in the two years. In not a single case can the differences between the constants for the same month in the two competitions for which data are

available be considered greater than those to be attributed to experimental errors.

While all the correlations between October pigmentation and the egg production of the individual months are negative in sign, they differ greatly in magnitude. Beginning with a correlation of about —.150 in November, the intensity of the relationship increases numerically to about —.250 in December, after which it falls to practically zero in March and April, and then increases in (negative) intensity rapidly to about —.750 in October.

The fact that roughly speaking the correlation increases in intensity as the two variables become more closely associated in time, suggests that the correlation demonstrated is of a purely physiological nature. The hypothesis that the growth of the egg abstracts certain substances—in the present case, yellow pigment—from the body tissue, or precludes its being deposited there, would at once account for the generally higher correlation between measures made at more closely associated periods of time.

If this view be the correct one, egg production must be regarded as the (relatively) independent variable, and intensity of pigmentation as the dependent variable. Egg production would then be looked upon as the chief proximate cause of the observed intensity of pigmentation.

For a detailed discussion of a number of lines of evidence for this view, the reader must consult preceding pages.

The fact that pigmentation has throughout this paper apparently been taken as the more fundamental character must not suggest that it has ever been considered by the authors to be such *physiologically*. Any such emphasis results merely from the fact that we have been seeking to determine the prediction value of a somatic character for use in the selection of birds characterized by high egg production without actually determining their record by trap-nesting.

Finally those who may be interested in the practical application of the results here secured must bear in mind the fact that the flocks from which our data were obtained represent a selected class of birds. Only groups of birds which are supposed to be the most promising are placed in the competition. The birds in the contest show, because of better breeding, better feeding and care, or both, a far higher annual egg production than those of the average flock. Unfortunately data of the kind presented here are not as yet available for the unselected class of layers.

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THE PROBABLE ERROR OF A DIFFERENCE AND THE SELECTION PROBLEM[1]

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In GENETICS for July, 1916, appears an interesting and suggestive paper by ACKERT (1916) on the effect of selection in Paramecium. The general logical method of this paper, with its insistence on the statistical presentation of adequate quantitative evidence, is altogether praiseworthy. And furthermore there will be little doubt in the mind of anyone who has followed recent genetic literature at all closely that the general conclusion reached is of a sort to be entirely satisfactory to the present writer. I cannot, however, permit a gross error in a particular biometric method, largely made use of in ACKERT'S paper, to pass without protest, because it seems to me to make the author's otherwise satisfactory general conclusion that selection is without effect, rest upon an extremely insecure statistical foundation.

At various places in his paper (pp. 390, 395, 402) ACKERT makes statements about probable errors of differences between means, calculated on the basis that the probable error of a difference is the sum of the probable errors of the quantities entering into the difference. Such is not the fact. It has long been known that the standard deviation of a difference between two constants is given by the following expression (cf. PEARL 1909).

Let $z = x - y$.

Then $\sigma_z = \sqrt{(\sigma_x^2 + \sigma_y^2 - 2r_{xy}\sigma_x\sigma_y)}$ - - - - - - - - - - - - - - - - - - (i),

where x and y denote any statistical constants, and z the difference between them. Also σ denotes the standard deviation of the variable indicated by its subscript, and r_{xy} is the coefficient of correlation between x and y. Now in ordinary cases of statistical comparisons, the constants compared are derived from distinct and separate samples, so that r_{xy} necessarily equals 0.[2] Equation (i) then becomes, of course,

$$\sigma_z = \sqrt{\sigma_x^2 + \sigma_y^2} \text{ - - - - - - - - - - - - - - - - - - (ii),}$$

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 103.

[2] One should never assume without careful consideration, however, that $r_{xy} = 0$ in any particular case. The possibilities in the way of unsuspected error correlations are large.

which, remembering that in a distribution of unit area the "probable error" is 0.6744898..... times the standard deviation, leads to the usual rule of statistical texts that "the probable error of a difference is equal to the square root of the sum of the squares of the quantities entering into the difference." ACKERT has apparently tried to simplify this rule still further by assuming that the square root of the sum of the squares of two quantities is the same as the sum of the quantities. Unfortunately it is not.

Now suppose we calculate correctly the probable errors of the differences in ACKERT's table 8 (p. 402) and see how the results then appear. Table 1 is a reconstruction of ACKERT's table 8, with the addition of (a) the probable errors of the differences, and (b) the quotient diff./P.E. diff., and (c) recalculated and corrected values of the probable errors of the means themselves. In only one case out of all the probable errors in ACKERT's table 8 was the probable error of a mean as printed found upon recalculation to be entirely correct. In most cases the errors concerned only the third place of figures, and evidently arose from the fact that he did not carry sufficient places of decimals in his intermediate calculations to give a correct value for the final place in the tabled results. In a few cases, as will be seen by comparison of table 1, with ACKERT's table 8, the probable errors of the means are grossly incorrect, due probably to some large undiscovered slip in the arithmetic. Of course in making the recalculations his values of the standard deviations had to be used, since he gives no frequency distributions from which they may be independently calculated, but only diagrams, too coarse to read accurate integral frequencies from. So then the values of the probable errors given in table 1 are correct to 3 places of decimals, on the assumption that ACKERT's standard deviations are correct to the same degree.[3]

From this enlarged table we note the following points:

1. In three out of the four experiments (viz., 2, 3 and 4) the progeny

[3] It is a disagreeable task to call attention to small arithmetical errors, but much American biometrical work is fearfully and wonderfully weak in its elementary arithmetic. If one tables constants to 3 places (or any other number of places) of decimals the presumption is that the results are *accurate as far as tabled*. Mathematicians follow such a code. If biologists are going to use mathematical methods they must eventually do the same thing. But how many biologists are there who even *know* how many places of decimals must be carried in intermediate computations to ensure that the second, third, fourth, or *n*th place in the final result shall be correct?

TABLE 1

ACKERT'S *results on Paramecium.*

	Length in microns				
	Group	Parents	Offspring	Difference	Diff./P.E. diff.
Group A Experiment 1	A_1	90	124.996 ± 0.283	0.650 ± 0.414	1.57
	A_2	162	124.346 ± 0.302		
Group B Experiment 2	B_1	162	179.540 ± 0.466	4.778 ± 0.618	7.73
	B_2	235	174.762 ± 0.406		
Group C Experiment 3	C_1	162	167.105 ± 0.479	3.071 ± 0.692	4.44
	C_2	198	164.034 ± 0.500		
Group D Experiment 4	D_1	135	125.307 ± 0.356	7.311 ± 0.504	14.51
	D_2	184	117.996 ± 0.357		

	Breadth in microns				
	Group	Parents	Offspring	Difference	Diff./P.E. diff.
Group A Experiment 1	A_1	36	53.050 ± 0.144	0.760 ± 0.209	3.64
	A_2	45	54.290 ± 0.152		
Group B Experiment 2	B_1	45	56.359 ± 0.200	1.281 ± 0.262	4.89
	B_2	54	57.640 ± 0.170		
Group C Experiment 3	C_1	36	66.093 ± 0.185	1.707 ± 0.297	5.75
	C_2	45	67.800 ± 0.232		
Group D Experiment 4	D_1	60	44.923 ± 0.200	3.288 ± 0.309	10.64
	D_2	64	48.211 ± 0.235		

population from the *shorter* selected parent is *significantly longer* than the population from the originally longer parent. The differences are so great in comparison with their probable errors in every one of these cases as to make the odds from 332 to 1 (in the case of experiment 3) to far above 1,000,000,000,000 to 1 (in the case of experiment 4) against their being accidental or due to random sampling (cf. PEARL and MINER 1914). Now in order to prove that selection was without effect the

means in the two compared groups in each case should be *the same,* within the limit of errors due to sampling. How far the facts are from such a condition is sufficiently evident from the above figures.

2. In the same three experiments (2, 3 and 4) the progeny population from the *broader* parent is significantly *broader* than the population from the narrower parent. The differences are so large in comparison with their probable errors that the odds against their being accidental range from about 1052 to 1, in experiment 2, to a magnitude which is far beyond human conception in experiment 4.[4]

3. Experiment 1 gave a result totally unconformable, when mathematically considered, with the other experiments. Here there is no significant difference in the mean lengths. The breadth means differ by a probably significant amount in the opposite direction to that in which the selection was made.

It is of course impossible for the present writer to hazard any opinion as to the cause of the statistically enormous differences which appear in ACKERT's experiments. He suggests (p. 395) that they may be "due to an uncontrolled factor in the environment." Probably this is true, but if it is, just what bearing on the selection problem do the results have? It seems very clear that if, in an experiment designed to test the effect of selection, there are environmental differences acting upon compared groups, so great that they cause differences of the relative magnitude exhibited in ACKERT's data, the results can by no possibility have any critical worth whatever in the discussion of the selection problem. They leave that problem in precisely the same status that it was before. This would seem to be exactly the fact in regard to the effect of selection in Paramecium. The work of JENNINGS (1908) demonstrated, so far at least as the strains with which he worked are concerned, that selection for size differences within the pure line in Paramecium is without effect. ACKERT's work neither confirms nor refutes that result.

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[4] The odds against a deviation 8 times the probable error are 1,470,588,234 to 1. Here we have a deviation *10.6* times the probable error!

CROSSING OVER OHNE CHIASMATYPIE?

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I

Es ist wohl nicht zu viel gesagt, wenn man behauptet, dass MORGANS und seiner Mitarbeiter Untersuchungen an Drosophila die wichtigste Bereicherung der Vererbungslehre in den letzten Jahren darstellt. Sie sind ein Musterbeispiel für ein zielbewusstes Handinhandarbeiten von Vererbungsexperiment und cytologischer Forschung und ihre Hauptergebnisse gehören jetzt schon zum wichtigsten Schatz unserer Wissenschaft. Wenn irgendwelche Arbeiten im Stande waren, auch die letzten Zweifler von der Richtigkeit der Chromosomenlehre der Mendelschen Vererbung zu überzeugen, so sind es diese. Diese Ueberzeugung soll uns aber nicht blind machen und verhindern, da Kritik anzulegen, wo es notwendig erscheint. Wenn dies im Folgenden geschehen soll, so tue ich es in der Ueberzeugung, dass die Tragweite der MORGANschen Resultate nur erhöht werden kann, wenn sie von Folgeschlüssen befreit sind, die nicht notwendig sind, und so bestechend und geistreich sie auch sein mögen, einer weiteren Vertiefung der Erkenntnis dadurch schaden, dass sie sie in einer bestimmten, aber nicht notwendigen Richtung festlegen.

Der auffallendste und imposanteste Schluss aus MORGANS Arbeiten ist natürlich der, dass er aus den Zahlenverhältnissen der "crossover" Klassen in den Zuchten auf die relative Lage der körperlichen Aequivalente der Erbfaktoren im Chromosom schliessen kann. Und dieser Schluss wieder basiert auf der Annahme, dass der in seinen Zahlenverhältnissen typische Austausch zwischen den homologen Chromosomen durch den Austausch von Chromosomensegmenten im Gefolge einer Chiasmatypie gegeben wird. MORGAN selbst ist sich natürlich der Tatsache bewusst, dass die Annahme von JANSSENS Theorie der Chiasmatypie, so weit die cytologischen Tatsachen in Betracht kommen, ziemlich in der Luft schwebt. Man könnte ihm trotzdem in der Verwendung dieser Hypothese, angesichts ihres Erklärungswerts, zustimmen, wenn sie nötig wäre. Aber das ist nicht der Fall. Und nicht nur dies, es erscheint uns sogar, dass die Chiasmatypiehypothese und die sich daraus ergeben-

den Konsequenzen in bezug auf die Lagerung der Faktoren im Chromosom ein Nachteil ist. Sie legt unsere Vorstellungen auf einen relativ einfach erscheinenden, grobsinnlichen Vorgang fest und belastet uns damit mit einer Kette, die unter Umständen verhindert, dass aus den gleichen Tatsachen noch weiterreichende Schlüsse gezogen werden können. Sie täuscht uns die Erreichung einer zweiten Stufe der Erkenntnis vor, während in Wirklichkeit nur die erste erreicht ist, und aus den zahllosen gleichberechtigten Möglichkeiten für die zweite, nur eine einzige, leicht sinnlich vorstellbare, heraus gegriffen ist. Es wird sogleich klar werden, was wir damit meinen.

Die erste Stufe, die unseres Erachtens durch MORGANS Experimente mit Sicherheit erreicht ist, ist der Nachweis, dass Faktoren zwischen den Chromosomen eines Paares ausgetauscht werden können und dass das Mass, in dem sie ausgetauscht werden, für je zwei oder mehr gegebene Faktoren unter gleichen äusseren Bedingungen ein typisches ist, variierend zwischen vollständiger "Linkage" oder Nichtaustausch und freier Spaltung oder beliebigem Austausch. Die zweite Stufe der Erkenntnis wäre dann der Nachweis der Kräfte, die dies quantitativ verschiedenartige Verhältnis des Austausches bedingen. Für MORGAN ist es die Chiasmatypie und die Entfernung der Faktoren im Chromosom, also morphologische Lagebeziehungen, die dafür verantwortlich sind. Dies ist der Schluss, den wir als unnötig nachweisen wollen, indem wir zeigen, dass für die Erklärung jener quantitativen Verhältnisse die gleichen Kräfte ausreichen, die überhaupt beim Aufbau eines Chromosoms aus Faktoren am Werk sein müssen, welcher Art sie auch seien. An die Stelle jener Schlussfolgerung wollen wir eine viel allgemeinere setzen, von der MORGANS Hypothese nur ein grobsinnlich gefasster Spezialfall ist. Er sieht in den unbekannten, quantitativ bestimmten Kräften des Austauschs eine entsprechende Entfernung der Faktoren im Chromosom. Es ist aber doch klar, dass man jede Proportion geometrisch als Entfernungen auf einer Geraden darstellen kann. Wenn diese Darstellung also im gegebenen Fall stets mit den Tatsachen übereinstimmt, so beweist das nicht etwa, dass nun wirklich Entfernungen auf einer Geraden hinter der Erscheinung als Ursache stehen, sondern es beweist nur, dass irgendwelche Kräfte im Spiel sind, deren relativer Effekt als Entfernungen auf einer Geraden dargestellt werden können. Wir glauben, dass es sehr wichtig ist, dies uns klar zu machen; denn während MORGANS Hypothese nur den allereinfachsten denkbaren Spezialfall in

Betracht zieht, erlaubt jene allgemeine Fassung nicht nur alle möglichen anderen Vorstellungen, sondern lässt auch die wichtige Möglichkeit zu, später einmal aus den beobachteten Zahlenverhältnissen Schlüsse auf die wirkliche Art der wirkenden Kräfte ziehen zu können, ähnlich wie man aus den bei Temperatur- und Variationsversuchen an Embryonen gewonnenen Zahlen auf den chemischen Charakter der zu Grunde liegenden Reaktionen schliessen konnte. Wir wollen somit beweisen—was eigentlich auch ohne besonderen Beweis klar sein sollte—dass aus den Crossover-Experimenten nur dies folgt, dass das Mass des Crossing over der Ausdruck irgend einer quantitativ variabeln Kräfte wirkung ist, die für die Zugehörigkeit eines Determinanten zu einem der Chromosomenpartner verantwortlich ist, eine Kraft deren relative zahlenmässige Wirkungen natürlich auch geometrisch als Abschnitte einer Geraden dargestellt werden können.

II

Morgans Schlussfolgerungen aus seinen Versuchen, und zwar sowohl die, die uns hier beschäftigen, wie alle anderen cytologischer Natur, basieren auf einer Reihe von Annahmen, die ein jeder Anhänger der Chromosomenlehre der Vererbung machen muss. Ueber sie wollen wir uns zuerst einmal klar werden. Da ist zunächst die Annahme der Individualität der Chromosomen, ohne die ja überhaupt eine Parallele zwischen Chromosomenverteilung und Faktorenspaltung nicht durchführbar ist. Sodann haben wir die Annahme, dass in jedem Chromosom mehrere und verschiedenartige Erbfaktoren enthalten sind. Für ihre Richtigkeit bringen ja gerade Morgans Untersuchungen so überzeugendes Beweismaterial bei. Sodann muss angenommen werden, dass die Lagerung der Teilchen, die den Erbfaktoren entsprechen, innerhalb des Chromosoms eine typische ist, ob wir sie uns nun linear angeordnet vorstellen oder nicht. Denn sonst wäre ein geordnetes "Crossing over" überhaupt nicht denkbar. Daraus folgt aber noch eine andere wichtige Annahme. Während der Kernruhe werden die Chromosomen körperlich desintegriert. Bei der nächsten Teilung finden sie sich aber wieder unter Wahrung der Individualität vor. Es müssen also irgend welche Kräfte im Spiel sein, die bei der Bildung der Chromosomen immer wieder jedem Partikelchen-Erbfaktor seinen Platz im richtigen Chromosom und am richtigen Platz

anweisen. Ob dies nun für gewöhnlich ausgesprochen wird oder nicht, sicher ist, dass jede Chromosomenhypothese auf dieser Vorstellung basiert.

Und nun bleiben wir einmal bei diesem letzteren Punkt. Da ist es zunächst klar, dass wir über die Art der Kräfte, die die richtige Sammlung der Partikelchen zum Chromosom bedingen, nichts wissen. Es mögen chemische Affinitäten sein, es mögen Wirkungen der Massenkraft sein, es mögen grobmechanische Dinge sein. Aber unter allen Umständen müssen sie spezifisch und typisch für jedes gegebene Partikelchen-Erbfaktor sein. Ist dies schon für irgend eine geordnete Lagerung der Teilchen im Chromosom nötig, so ist es gewiss so für eine geordnete lineare Lagerung, mit der auch Morgan arbeitet. Für unsre weiteren Auseinandersetzungen ist es gänzlich gleichgiltig, wie wir uns die typische, geordnete Lagerung vorstellen. Und so ist es das Einfachste, dass wir uns auch die Dinge als lineare Anordnung der Partikelchen versinnlichen, da es die einfachste graphische Darstellung erlaubt; auch der Chemiker benutzt ja flächenhaft angeordnete Symbole anstatt der verwickelteren stereometrischen Vorstellung, ohne sie deshalb als eine Realität zu nehmen. Wenn nun also die Partikelchen sich zu einer typischen Reihe spezifischer Anordnung immer wieder zusammenfinden sollen, so müssen, wie gesagt, die wirkenden Kräfte für jedes einzelne in Bezug auf seine Nachbarschaft typisch sein. Wenn wir uns das versinnbildlichen wollen, so können wir die Kräfte, die einem Partikel die Lage neben einem andern und nur neben diesem anweist, als eine Wirkung bestimmter Quantität darstellen und graphisch könnten wir uns dann die Festlegung eines bestimmten Platzes im Chromosom für ein Partikelchen so veranschaulichen wie es Fig. 1 wiedergiebt. Die Kraft, die ein Partikelchen-Erbfaktor an sein Chromosom kettet ist durch einen rechteckigen Anker wiedergegeben, dessen Grösse der Quantität dieser Kraft entspricht. (Wir "verankern" den Faktor an seinem Chromosom im Interesse der graphischen Darstellung; sachlich kann das aber eben so gut die Verankerung an seinem Nachbar oder sonst etwas bedeuten). In der Figur 1 sind somit die Erbfaktoren *ABCD* enthalten, die ihre richtige Lagerung in dem betreffenden Chromosom—die hier linear dargestellt ist aber ebenso gut irgend eine stereometrische Form haben könnte—den spezifischen Kräften von der spezifischen Quantität und Qualität *w x y z* verdanken. Wenn wir nun das entsprechende Chromosom einer Form darzustellen hätten, die an Stelle von *B* nur *b* enthält, so könnten wir es entweder unter wörtlicher Auslegung der presence-

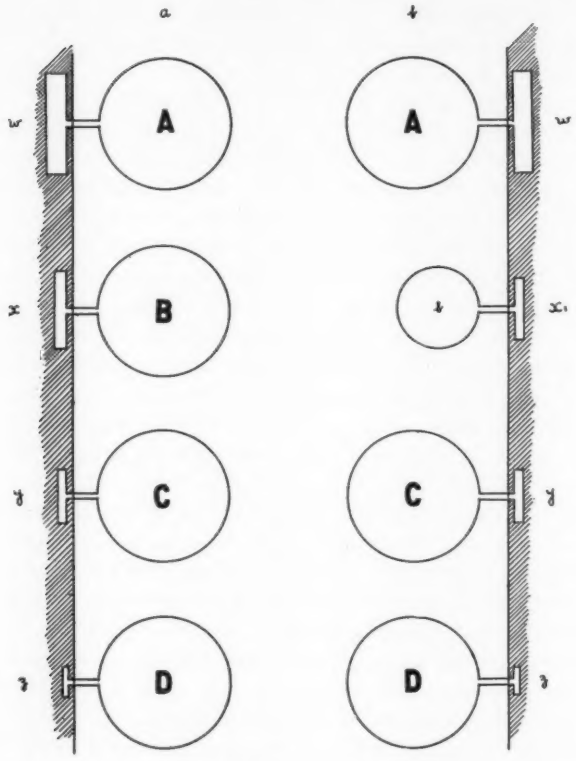

FIG. 1

absence Theorie so machen, dass hier *B* fehlt, oder auch einen andersartigen Faktor *b* einfügen, dessen Andersartigkeit sich auch in seiner andersartigen und spezifischen Verankerung zeigt also x_1 statt x. Sachlich ist es gleichgiltig, welche Darstellung wir wählen, denn schliesslich sind ja beide nur differente Anschauungsformen von presence-absence. Die letztere ist bequemer zu handhaben und daher in Fig. 1 *b* angewandt. Wenn wir nun den Bastard *Bb* vor uns haben, so werden also auch bei ihm bei der Chromosomenbildung die Faktoren *B* und *b* an ihren richtigen Platz in dem richtigen väterlichen oder mütterlichen Chromosom sich einfinden und Fig. 1 wäre dann eine Darstellung eines Chromosomenpaares dieses Bastards. Wie schon gesagt, hier haben wir

nicht das geringste Neue ausgesagt, sondern einfach die selbstverständlichen Voraussetzungen der Chromosomenlehre uns graphisch klar gemacht.

Daraus folgt nun ohne Weiteres das Folgende: Sind die Kräfte x und x_1 quantitativ so verschieden, dass sie nicht vertauscht werden können, so können die Faktoren *B* und *b* stets nur wieder sich in ihrem ursprünglichen Chromosom einfinden; im Vererbungsversuch erschienen sie also vollständig "linked" mit dem Rest der Faktoren. Wären die Kräfte x, x_1 aber so ähnlich, dass sie vollständig freien Austausch der Faktoren gestatteten, die sich somit beliebig in jedem der beiden elterlichen Chromosomen an dem betreffenden Platz einfinden könnten, so müssten *Bb* eine reine Mendelspaltung zeigen, die nicht von einer Spaltung von in differenten Chromosomen gelagerten Faktoren zu unterscheiden wäre. Wären endlich aber die Kräfte x, x_1 variabel und ein Überschneiden der Curven fände statt, so hätten nur die in dem gemeinsamen Kurvenbezirke gelegenen Fälle die Möglichkeit ihren Platz in dem einen oder anderen Chromosom zu finden, d.h., zu cross over. Diese drei Möglichkeiten können wir uns an den nebenstehenden Variations kurven für die Kräfte x, x_1 ohne Weiteres klar machen (Fig. 2),

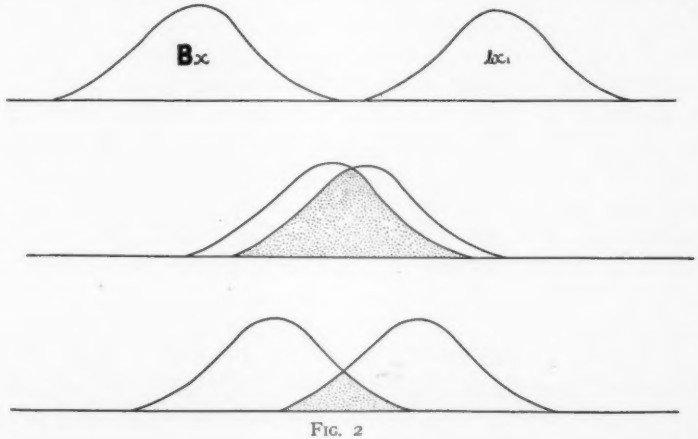

FIG. 2

wobei natürlich die einfachste Annahme über die Art der Variation gemacht ist. Die Zahl der Fälle des Hinüberkreuzens eines Faktors wäre aber proportional der Grösse des gemeinsamen Kurvenbezirks, und bei

zwei Faktoren, die allein ja das Resultat erkennen liessen, proportional der Combination beider Kurvenbezirke. Und wenn, wie selbstverständlich, die Werte x, x_1, etc., zu den typischen Qualitäten der Faktoren B, etc., gehören, so muss auch in diesem Fall für jede Faktorenkombination der Prozentsatz des Hinüberkreuzens unter gleichen Bedingungen konstant sein. So zeigt es sich, dass die ganze Erscheinung des Crossing over eine logische Konsequenz aus der Individualität der Chromosomen ist, somit keine weitere Hilfshypothese zu ihrer Erklärung nötig ist. Es zeigt ferner, dass der typische Prozentsatz der crossover Klassen ganz allgemein der Ausdruck einer entsprechend typischen Verschiedenheit der den Chromosomenaufbau aus den Einzelfaktoren bedingenden Kräfte ist; und somit gar kein Bedürfnis vorliegt, an Stelle der Kräfterelationen, deren Wirkung natürlich auch geometrisch als Abschnitte einer Geraden dargestellt werden können, die ganz bestimmte Vorstellung der Chiasmatypie und räumlichen Entfernung zu setzen.

Hier könnte nun noch die Frage aufgeworfen werden, ob ein derartiger Faktorenaustausch nicht eben so gut in den diploiden Keimbahnzellen stattfinden müsse, wie in den Geschlechtszellen vor den Reifeteilungen. *A priori* lässt sich dies in der Tat nicht leugnen. Sachlich würde das aber nichts ändern, sondern nur bedeuten, dass das Mass des Crossover eine Funktion von zwei Variabeln, nämlich sowohl der betreffenden Verankerungskräfte als auch der Zahl der somatischen Keimbahnteilungen ist. In Fällen, in denen die Crossoverzahlen in verschiedenen Versuchen verschieden ausfallen (etwa bei Antirrhinum) mag tatsächlich diese Annahme die Erklärung liefern. Sonst ist sie unnötig und daher empfehlenswert nur mit einem einmaligen Austausch in der Synapsis und Wachstumsperiode zu rechnen.

Als wichtig erscheint in diesem Zusammenhang auch das folgende. Es ist bemerkenswert, dass bei Drosophila der Faktorenaustausch nur im weiblichen Geschlecht stattfindet, in anderen Beispielen nur im männlichen oder in beiden. Wenn der Austausch bedingt wird durch die transgredierende Variation zweier Kräfte, so sollte diese abhängig sein von Aussenfaktoren. Die Aussenwelt für die Chromosomen is zunächst der Kern. Tatsächlich gehen während der den Reifeteilungen vorausgehenden Wachstumsperiode im Keimblässchen Umwälzungen vor sich,

die die Variationsursachen abgeben könnten. Das Crossing over fände dann bei dem Neuaufbau der Chromosomen zu den Reifeteilungen statt, und eventuelle Verschiedenheiten darin zwischen den Geschlechtern wären zu erklären aus den Bedingungen dieser Periode, die Variation begünstigen oder nicht. Damit stimmt auch die Tatsache überein, dass die Crossoverzahlen durch äussere und innere Einflüsse (Altern bei Drosophila) verändert werden können. Dies ist natürlich auch nur eine Hypothese, die für die Gesamtbetrachtung nicht wesentlich ist.

Um Missverständnisse zu vermeiden sei an dieser Stelle nochmals folgendes hervorgehoben. Es ist nicht meine Absicht, an Stelle von MORGANS Hypothese eine andere zu setzen, oder gar seine Darstellung als grobsinnliches Schema zu verwerfen, und dann durch Aufstellung eines anderen Schemas denselben Fehler zu begehen. Das, was ich beweisen will, ist vielmehr, dass die Tatsachen auf Grund der von jedermann anerkannten Voraussetzungen der Chromosomenlehre verstanden werden können; dass dieselben Kräfte, die die Chromosomenindividualität bedingen, auch für die Erklärung des Crossing over ausreichen; ferner, dass wir für die Wirkung dieser unbekannten Kräfte verschiedene diagrammatische Darstellungen wählen können, die der graphische Ausdruck von Zahlenrelationen sind; und sodann, dass wir eine passende graphische Darstellung nicht mit der Wirklichkeit verwechseln sollen, da wir uns dadurch den Weg für weitere Erkenntnis versperren, besonders für eine solche physikalisch-chemischer oder dynamischer Natur.

III

Die hier entwickelten Anschauungen sind von mir schon mehrfach, für den Fachmann verständlich, angedeutet worden. JANSSENS Chiasmatypie-Theorie sollte ja eine Erklärung für die Möglichkeit des Vorhandenseins mehrerer spaltender Faktoren in einem Chromosom geben. Die crossover Theorie steht aber auf der gleichen Basis. Schon 1911 habe ich eine Idee entwickelt, wie das Vorhandensein mehrerer selbstständig spaltender Faktoren in einem Chromosom erklärt werden kann, der prinzipiell derselbe Gedankengang, wie der hier durchgeführte, zu Grunde liegt. Die damaligen Ausführungen hatten aber den Nachteil, dass sie mit der Annahme der end-to-end Conjugation verquickt waren und auch mit einer zu wörtlichen Auslegung der presence-absence Theorie. Sie haben daher auch keine weitere Beachtung gefunden.

Diese früheren Äusserungen haben wohl MORGAN, MULLER, STURTEVANT u. BRIDGES (1915) im Sinn, wenn sie von der Anschauung "einer

Anzahl Genetiker" sprechen,[1] die das Crossover mit dem Chromosomenaufbau aus Partikelchen in Zusammenhang bringen. MULLER (1916) geht in seiner neuesten Arbeit etwas näher auf diesen Punkt ein. Da im Vorhergehenden und Folgenden alle von ihm angeführten Punkte ohnehin besprochen werden, brauchen wir hier nicht noch einmal darauf zurück zu kommen. Aber es erscheint doch wünschenswert, noch im Speziellen zu zeigen, dass tatsächlich die Versuchsergebnisse in der hier durchgeführten Weise erklärt werden können.

Nehmen wir an, wir hätten in einem Versuch zu tun mit den elterlichen Faktoren *A B* und *a b*. Bei dem Aufbau der Chromosomen zur Reifeteilung gelangen also normaler Weise *A B* und *a b* in die homologen Chromosomen. Wenn die Kraft, die ihnen ihren Platz anweist bei *A* und *a* oder *B* und *b* sehr verschieden ist, tritt völlige "Linkage" ein. Ist sie aber nur soweit verschieden, dass die Grenzfälle transgredieren, dann tritt Crossing over ein. Nehmen wir nun an, dass für die Faktoren *A a* die elterliche Lage im Chromosom 3 mal so oft eintritt als das Ueberkreuzen, also unter 4 Fällen 3 normal sind; ferner, dass für die Faktoren *Bb* das gleiche Verhältnis 5 : 1 sei. Dann wird, falls dies nur in einem Geschlecht stattfindet, das Verhältnis der elterlichen Kombinationen zu den crossover Klassen *Ab* und *aB* gleich 16 : 8 sein oder 50 prozent. Wenn wir anstatt 3 : 1 und 5 : 1 allgemein setzen p_a : 1 und p_b : 1, so giebt uns die Formel $\frac{100\,(p_a+p_b)}{(p_a+1)\,(p_b+1)} = cr$ die crossover Klassen für *AaBb* in Prozent wieder. Empirisch gefundene Werte für cr könnten natürlich auf sehr verschiedenen Werten von p_a und p_b beruhen. Wenn aber noch ein drittes Faktorenpaar *Cc* hinzu kommt, so legen die crossover Prozente für *AB, AC* und *BC* die Werte p_a p_b p_c fest. Nehmen wir nun einmal eine Serie von Faktorenpaaren *Aa Bb Cc Dd,* etc., und setzen für sie angenommene Werte für p_a, p_b . . ., nämlich:

$p_a = 3$
$p_b = 4$
$p_c = 10$
$p_d = 20$
$p_f = 50$
$p_l = 1000$

und rechnen die danach zu erwartenden crossover Prozente für die verschiedenen Faktorenkombinationen aus, dann sind

[1] Auch STOMPS (1912) hat einmal ähnliche Äusserungen veröffentlicht.

cr $AB = 35.0\%$ cr $BC = 25.5\%$ cr $CD = 13.0\%$ cr $DF = 6.5\%$
cr $AC = 29.5\%$ cr $BD = 22.9\%$ cr $CF = 10.7\%$ cr $DI = 4.9\%$
cr $AD = 27.4\%$ cr $BF = 21.2\%$ cr $CI = 9.9\%$ cr $FI = 2.1\%$
cr $AF = 26.0\%$ cr $BI = 20.1\%$
cr $AI = 25.0\%$

Wenn wir dann diese Werte graphisch nach MORGANS Vorgang als Distanzen auf einer Geraden darstellen und dabei, wie MORGAN es tut, die kürzesten Strecken als massgebend nehmen, erhalten wir:

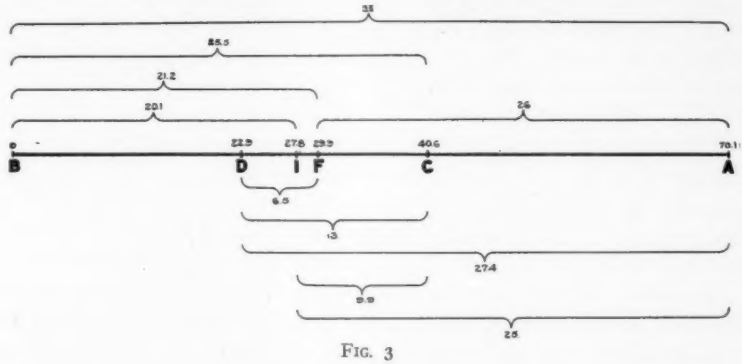

FIG. 3

Stellen wir nun daneben ein analoges Schema nach STURTEVANTS (1913) Untersuchungen über die Drosophila-Faktoren *B, CO, P, R, M:*

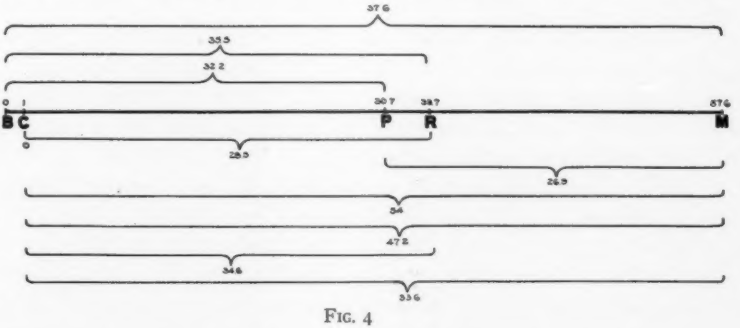

FIG. 4

Dies letztere soll die folgenden Gesetzmässigkeiten zeigen: Wenn es sich um kleine Distanzen handelt, giebt die Addition zweier Teilstrecken ziemlich genau den für die ganze Strecke berechneten Wert, z.B., $BP=32.2$, $PR=3$ und $BR=35.5$. Analog wäre in unserem Schema

BI=20.1, *IF*=2.1, *BF*=21.2; *AI*=25.0, *ID*=4.9, *AD*=27.4. Wenn es sich um grössere Distanzen handelt, giebt die Addition der Teilstrecken eine gröszere Summe als die Berechnung des Gesammtdistanz, z.B., *B, CO, P, R, M*=57.6, *BM*=37.6, oder *CO, P, M*=56.6, *COM*=54 resp. 33.6 resp. 47.2. Dem steht gegenüber im ersten Schema *B D I F C A*=70.1, *BA*=35.0; oder *B D I F C*=40.6, *B C*=25.5. Daneben finden sich aber noch allerlei nicht besonders hervorgehobene Inkongruenzen, z.B., bei STURTEVANT *CR*=28.5, *CP*=30, also eine Summe kleiner als eines der Teilstücke. Ebenso *CM*=33.6 aber *CR*=34.6. Bei uns entspricht dem *BD*=22.9, *BI*=20.1. Da *DI*=4.9 so würden wir, wenn nur diese 3 Werte bekannt wären, *I* zwischen *B* und *D* setzen und es stimmte dann. Das Gleiche wäre aber der Fall, wenn STURTEVANT nur die drei obigen Zahlen hätte. Ferner zeigt es sich, dass man verschiedene Werte für die gleiche Strecke bekommt bei verschiedener Art der Berechnung. So bei STURTEVANT für *BM* aus *BC*+*CP*+*PR*+*RM* =57.6; aus *BR*+*RM*=59.4; aus *BO*+*OM*=48.4; aus *BC*+*CM*= 34.8, etc. Dem entspricht im ersten Schema für *BA* aus *BD*+*DI*+ *IF*+*FC*+*CA*=70.1; aus *BI*+*IA*=45.1, aus *BC*+*CA*=55.0, etc.

In gleicher Weise könnte man natürlich auch ein double crossover Experiment berechnen und erhielte z. B. für den Versuch *BDC* die Zahlen

67% non-crossover
10% crossover *DC*
20% crossover *BD*
3% double crossover *BDC*

Es sei dies aber nicht weiter ausgeführt, einmal, weil wir glauben, dass die STURTEVANT'schen Vergleichszahlen auf Grund einer falschen Formel berechnet sind, und sodann weil es, wie so oft schon hervorgehoben, gar nicht unsere Absicht ist, das hier benutzte Schema an Stelle des MORGANschen setzen zu wollen.

MORGAN weist nun noch als besonders beweiskräftig auf die Tatsache hin—inzwischen von MULLER im einzelnen ausgearbeitet,—dass bei der Spaltung von Bastarden von der Zusammensetzung *ABCDEFGabcdefg* immer ganze Faktorengruppen beisammen bleiben, also meist single Crossing over, nur selten double und triple Crossing over eintritt. Eine Berechnung nach unserer Formel zeigt, dass auch dies als eine mathematische Konsequenz daraus abgeleitet werden kann, wie ja schon die Berechnung für das double Crossover zeigt. In MULLERS—zweifellos höchst schwierigen—Experimenten findet sich bereits für triple Crossing

over nur 1 Individuum. Nur bei viel grösseren Zahlen könnte man also die höheren crossover Klassen erwarten. Es braucht schliesslich wohl kaum hervorgehoben zu werden, dass der Erklärungswert von MORGANS Hypothese in Bezug auf multiplen Allelomorphismus und ähnliche Erscheinungen nicht dadurch berührt wird, wenn statt "Locus" Kräfterelation steht.

Zum Schluss dieses Abschnitts noch eine Bemerkung. Es könnte jemand auf den Gedanken kommen, nach meinen Auseinandersetzungen die Auflösungsformel zu berechnen und danach die Werte p der obigen Formel für die von MORGAN gelieferten Zahlen zu berechnen, und dann vielleicht Inkongruenzen im Resultat als Widerlegung der hier vorgebrachten Anschauungen aufzuzeigen. Das wäre aber ein grobes Missverständnis. Ich habe, um meine These durchzuführen, möglichst einfache mathematische Voraussetzungen angenommen. Es liegt mir aber durchaus fern zu behaupten, dass gerade diese der Wirklichkeit entsprechen. Im Gegenteil ist es ja meine Hoffnung, dass die Betrachtung der empirischen Zahlen umgekehrt einmal die richtige Formel für die zu Grunde liegenden Kräfte und damit ihre physikalisch-chemische Zuweisung ermöglichen werde. Das, um was es sich mir handelt, ist vielmehr, wie schon oben gesagt, zu zeigen, dass es besser ist, sich nicht auf die grobsinnlichen Anschauungen über die Lage der Faktoren im Chromosom festzulegen, sondern MORGANS diagrammatische Darstellung nur als eine geometrische Ausdrucksform für Kräfterelationen zu nehmen, deren Wesen zukünftiger Erkenntnis vorbehalten bleibt.

IV

Ist die Möglichkeit einer Erkenntnis dieser unbekannten Kräfte nun etwas in unendlicher Ferne liegendes? Ich glaube nicht. Und damit begeben wir uns nun auch auf den Weg der Hypothese. Wenn wir auch noch keine definitive Kenntnis darüber besitzen, was die Erbfaktoren darstellen, so machen eine Reihe neuer Arbeiten (z.B. LOEB u. CHAMBERLIN 1915, ONSLOW 1915, GOLDSCHMIDT 1916) es wahrscheinlich, dass sie etwas mit der Gruppe der Enzyme zu tun haben. Nun ist es ja eine unter Morphologen weitverbreitete Anschauung, dass Erbsubstanz chemisch mit Chromatin identisch sei. Ich habe dies, angesichts der cytologischen Tatsachen über die Umwandlungen des Chromatins in den Geschlechtszellen nie recht glauben können. Und auch die physiologischen Chemiker haben gewichtige Gründe dagegen. Nun findet man aber in der Fermentliteratur die Tatsache verzeichnet, dass einmal die

Enzyme besser Schädigungen widerstehen in Gegenwart von Nucleoproteiden, sodann, dass Oxydasen ebenso wie hydrolytische Fermente oft an Nukleoproteide gebunden sind. So liegt der Gedanke nahe, dass die Aufgabe des Chromatins es ist, die Vererbungsenzyme zu adsorbieren, als ihr Skelet zu dienen.[1] Sollten nicht vielleicht hinter den Variabeln und Konstanten des Crossing over die Variabeln und Konstanten der Adsorptionsgesetze stecken? Schon eine oberflächliche Orientierung in diesem so anziehenden Gebiet (s. etwa die Bücher von BAYLISS 1911, BECHHOLD 1912, MICHAELIS 1909, COHNHEIM 1912, EULER-POPE 1912) zeigt, wie aussichtsvoll eine eingehende Betrachtung dieser Beziehungen ist. Es sei nur erwähnt, welches Licht eine derartige Betrachtungsweise auf die typischen Oberflächenwandlungen des Chromatins während der Synapsis und Wachstumsperiode werfen könnte. Und der Weg hier weiterzukommen ist sicher ein sehr einfacher. Exacte Untersuchungen über den Einfluss verschiedener Temperaturen auf die Crossoverzahlen könnten vielleicht schon die entscheidenden Werte liefern.

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[1] Ich hatte vor mehr als einem Jahr das Vergnügen, diese hier in wenigen Worten angedeuteten Anschauungen über die chemische Basis der Vererbung A. P. MATHEWS auszuführen. Worauf er mich darauf hinwies, dass er genau die gleiche Anschauung in einem im Drucke befindlichen Werk ausgesprochen habe. Dies Buch (Physiological Chemistry, New York, 1915) ist inzwischen erschienen und enthält p. 175-182 die betreffenden sehr interessanten Ausführungen.

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